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THE DEVELOPMENT OF DRAINAGE SYSTEMS AND THE DYNAMIC CYCLE.*

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INTRODUCTION.

The present study looks at streams from the dynamic viewpoint.[1] It goes without saying that the forces at work on the lands of the earth are just as important in physiography as are the results brought about by those forces.

The concept of age, applied to valleys in a geomorphologic sense, has been carried over on occasion and applied to streams in such a way as especially to emphasize change of velocity and its results. A stream is never young, never mature, and never old in a strictly dynamic sense, for the processes, although they vary in intensity, vary little if at all in quality. However, a general view of streams or a combination of them reveals a certain cyclic sequence of events which it is the purpose of this paper to trace in orderly fashion. This sequence of events has been called the dynamic cycle.

The first hints of the dynamic cycle were observed on a hillside during a rainstorm. A fairly flat surface on rather compact material passed through enough of a miniature drainage cycle from the beginning of interlacing rills to the formation of master streamlets to give a momentary glimpse of the various steps in the cycle. Nothing further was done with the idea until the problems presented by the drainage and the land forms of southeastern Ohio suggested that a return to, and an intensive study of, the fundamental characteristics of stream development might throw light on the origin and history of the

*Presented before the Geological Society of America at Washington, D. C., December 28, 1929.

[1]Dual Nature of Physiography. Science, Vol. 72, 3–5, 1930.

drainage and also facilitate an understanding of the geomorphologic history. The present paper is one of the results of that study.

Subsequent field work included the further study of portions of the cycle passed through in miniature, and rather extensive observation during portions of four field seasons. The many different steps in the development of a drainage system may be observed separately on a large scale and later fitted together into an orderly sequence. Obviously the time required for the entire course of the cycle is too long to permit of direct observation.

An attempt has been made to follow the inductive method from the original observations to those made later and the whole tested and supplemented for synoptical reasons by map study. The United States Geological Survey topographic sheets of the eastern part of the country were consulted, about two hundred of the maps selected, and the drainage traced off. From these the illustrations here included were chosen to represent to a fair degree the sequence of events in the evolution of a drainage system. Maps of the late phases of the cycle were found in a region where the elevation of the level of base-level advanced the cycle sufficiently to give adequate illustrations.

The drainage cycle[2] falls naturally into two main sequential stages—extension and integration. Extension includes the sequence of events from initiation of the drainage system (in many cases the initiation of certain activities) until it, as a system or branchwork, completely occupies the basin. Integration includes the sequence of events from maximum extension to and through the emergence of master streams or master tributaries.

The scheme of development here presented will be given in a fashion as nearly ideal as possible, since departures or variations from the ideal for one reason or another will then be the more easily recognized and understood. The main body of the paper will trace the steps in the dynamic cycle and the discussions will consider some of the relationships between streams and their environment.

Assumptions and Definitions. — The initial assumptions include a certain uniformity of lithology, a simplicity of rock

[2]A summary view of the nearly ideal cycle appeared in the Geographical Review, July, 1931.

structure, and a humid climate like that of the eastern United States.

Any stream or branchwork of streams with a common point of discharge constitutes a drainage system. Rainwash from the dynamic standpoint includes all rain water that has not concentrated into definite streams which, after such concentration, form an organized part of a stream system.

The vertical distance through which rainwash travels on the ground is called the drainage relief and the ratio of the vertical to the horizontal distance covered at the same time is called the drainage ratio.

Acknowledgments.—The writer wishes to acknowledge his indebtedness to the Research Committee of the Graduate School of Ohio State University for a grant of funds with which he secured a research assistant to aid in the office work and the preparation of maps. He is also indebted to the Geological Department of Yale University, the Ohio Geological Survey, and the Department of Geology of Ohio State University for the use of maps and for office supplies. Sincere thanks are due these several organizations.

EXTENSION.

Initiation of the Drainage System.—The early and the late phases in the cycle are perhaps the most difficult of all to observe, to find on maps, and to picture mentally. Small scale observations give the best results, although on a very small area rainwash tends to overshadow the concentration of water into rills.

Figure 1 indicates what may be expected at the start of extension when drainage begins to be concentrated along definite paths. A number of the streams end without uniting into, or joining, a main, and swamps in some cases conveniently mark the courses of future streams. A large percentage of the surface lacks conspicuous channel-ways for the disposal of rain water. Though the coast has been drowned and the ground water surface has been elevated, yet the hints concerning the initiation of a drainage system appear clearly.

The streams on Figure 2 show a better degree of organization than those on Figure 1; they also show the disappearance in large measure of the indecision and hesitancy of pre-extension. Essential features of the future system have become apparent, although a few streams still end indefinitely. The blank

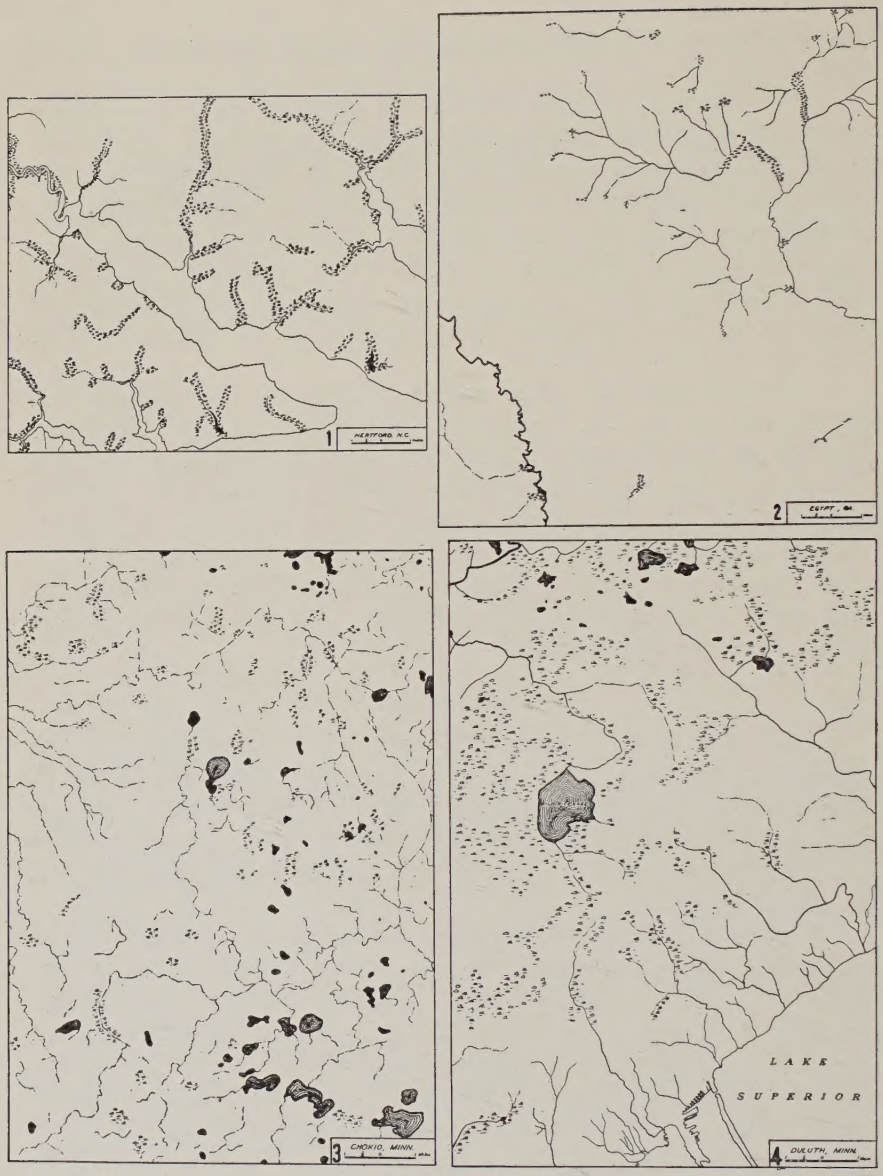

FIG. 1. The initiation of drainage systems; almost pre-extension for the most part.
FIG. 2. The start of dendritic extension. Swamps occur on uplands and lowlands. The probable role of swamps as indicating the courses of future streams is well shown on the central north-south strip of the Folkston, Georgia-Florida, topographic map.
FIG. 3. The first efforts toward organization and extension on a recently glaciated surface.
FIG. 4. The start of elongation. Poor organization. Both headward and mouthward elongation.

areas contain numerous shallow linear swamps which as features preceding actual streams are particularly well shown in the central part of the Folkston, Georgia-Florida, map.

Some parts of the Chokio, Minnesota, sheet (Figure 3) show the first efforts of the run-off to concentrate along definite paths, the first efforts toward organization on a recently glaciated surface. The inland part of the Duluth map (Figure 4) shows much the same condition save that, the topographic details being less minute than on the Chokio sheet, the initial stream courses are far less numerous, and hence the advance of the drainage cycle appears to be less rapid but more systematic.

Discussion.—Although rainwash dominates the time particularly before and during initiation, most of the land surface of the earth never leaves the rainwash stage. It is the task of a drainage system during extension to reduce the horizontal distance of rainwash travel to as small an amount as possible. From an areal standpoint, therefore, rainwash possesses far more importance than the streams to which the water is contributed.

The discovery of an ideal beginning for a drainage system, were such a thing possible, would be of great interest and utility. Four methods of origin come to mind: (1) headward growth of streams from what is commonly called the "gully stage," (2) the headward and mouthward growth and union of indefinite stream-ways into a unified stream discharging into another stream or body of standing water, (3) mouthward growth, and (4) combinations of the first three. The streams emptying directly into Lake Superior on Figure 4 appear to illustrate method (1), as do those on the north portion of Figure 5 neglecting drowning. The making of a hillside gully is a very common illustration of the first method, but many such gullies actually constitute in the end a phase of stream development by the second method.

The origin of a valley and the origin of a stream may differ to a considerable degree if the two be divorced temporarily. Part of the rain falling on a uniformly sloping area forms the run-off which attains sufficient volume to make definite streams long before the edge of lowest elevation is reached. At some place between the higher and lower edges, but closer to the upper, streams will normally begin.[3] Conspicuous gullies,

[3]See for instance: Marr, J. E. The scientific study of scenery. London, 1926. Pp. 72–75. Wentworth, C. K. Principles of stream erosion in Hawaii. Journ. Geol., Vol. 36, 398. 1928.

in contrast, tend to form at the lower edge and thence lengthen upstream in such fashion as to produce a break in the longitudinal profile of the valley. Profile breaks like these testify to a certain lack of simultaneity in the origin of a stream and the origin of a definite valley. They are by no means uncommon features and of course come to mind at once in relation to rejuvenated streams. A topographical and historical analysis of the short streams to Lake Superior on Figure 4 reveals the fact that their mouths have been elongated by lowering of the lake level (method 3) and their heads have been lengthened partly by means of method (1) and partly by means of method (2). In truth, the question may be raised whether any stream branching away from a main ever attained full size solely by wash at the gully head or, for that matter, by any single method of growth.

The streams on the remainder of Figures 4 and 5 and also those on Figure 3 subscribe to method (2) in origin. Rain falling on a new land surface seeks out all low places and the discovery of sloping linear depressions permits the formation of incipient streams. The union of such embryonic streams with each other or with an established waterway marks the origin of a definite stream (but not necessarily an erosional valley in entirety) and the beginning of the stage of extension.

In conclusion it may be said that many local streams and small tributaries have with little doubt been started from the "gully stage," though the gully is far more important in the history of a valley than in the development of the stream; and that most of the larger streams and the chief parts of drainage systems have originated in a more complex fashion than implied in the development of a gully.

Initiation on the whole is a time when such streams as do exist lack organization, when hesitation and indecision rather than systematized invasion of the land governs the run-off, and when rainwash overshadows all other processes. Initiation refers not only to the beginning of streams but also, and more especially, to the beginning of extensional activities. A continuation of these activities constitutes the stage of extension.

Elongation of Streams.—Elongation refers to all manner of stream lengthening. The first hints of systematic elongation indicate the existence of extension. Two directions of lengthening may be observed: headward into unoccupied land inherited

from a formative agency, as glaciation, and mouthward over a newly emerged area.

All maps in the first part of the paper show elongation of one type or another. The main streams on Figure 6 not only show headward elongation, but also suggest the possibility of future competition which will arise because of such elongation. Additional examples may be seen on Figures 1, 2, 4 and 5.

Growth in the opposite direction, mouthward, is much less emphasized in geologic literature and less well developed in our ideas of stream history. Mouthward elongation has been called "progression" by Doctor W. Armstrong Price,[4] the progressive river being one "which grows outward across a rising coastal plain." However, the type of lengthening here considered is far more general in application, referring to all lengthening accomplished in the mouthward direction as the following examples indicate. The streams flowing into the Glacial Lake Agassiz lengthened mouthward as the lake contracted and withdrew to northward. Figure 7 shows the result at one locality. Such direction of growth was not always exactly parallel to the older part of the stream; in some cases the elongated portion made high angles with the original course[5] or even reversed its direction.

In fact mouthward elongation has been very common in the areas contiguous to the Great Lakes. Postglacial streams, independent of preglacial channels,[6] now flow over the beds of glacial lakes into the present Lake Superior, having entered Lake Duluth and successively afterward, Lake Algonquin and the Nipissing Great Lakes prior to the existence of Lake Superior. St. Louis River likewise lengthened its lower course[7] to follow the receding waters of Lake Duluth. The streams along the western and southern margins of Lake Erie have had the same history, illustrated in one case by the Fremont, Ohio, sheet (Figure 8).

Elongation serves to get the stage of extension under way, to produce a skeletonized drainage system, and by so doing, to eliminate the initial abbreviated streams.

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[4]Personal communication, March 26, 1930.

[5]Upham, Warren. The Glacial Lake Agassiz, U. S. Geol. Survey, Mono. 25, 19–20, 54–57; Pls. 3 and 25. 1896.

[6]Leverett, F. Moraines and shore lines of the Lake Superior region, U. S. Geol. Survey, Prof. Paper 154-A, 8. 1929. Plate 2 shows the many short streams entering Lake Superior.

[7]Ibid, 10.

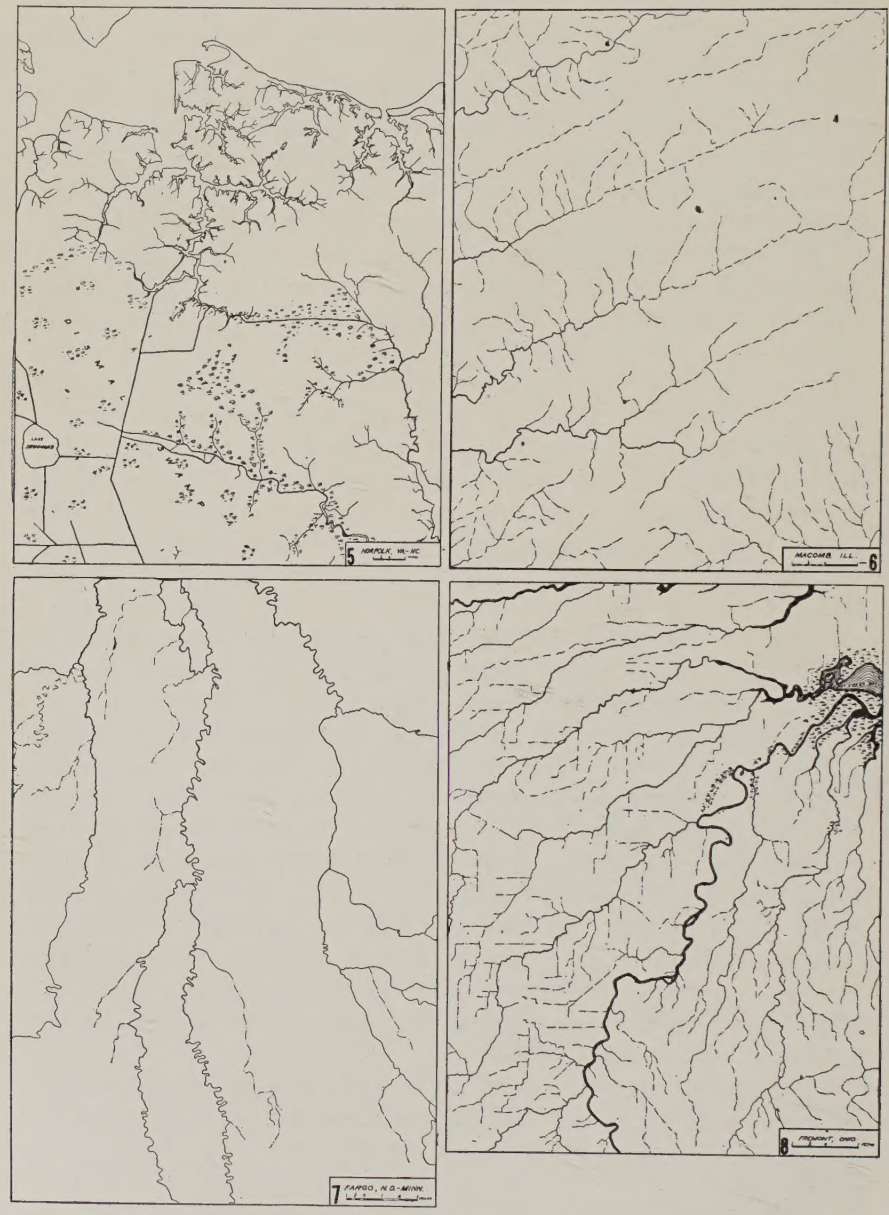

FIG. 5. Early extension and headward elongation.
Fig. 6. The stage of extension on a drift plain; elongation fairly complete, elaboration started. Parallel headward elongation.
FIG. 7. Early extension on a lake plain. Parallel mouthward elongation. Elaboration barely begun.
FIG. 8. Mouthward elongation over a lake plain.

Discussion.—The word "extended" has been applied[8] on several occasions to rivers lengthened mouthward. Since the term does not enjoy common usage, its application, in the altered form "extension," has been broadened for use in connection with the first stage of the dynamic cycle, and the more simple designation lengthening, or elongation, employed for linear growth.

Mouthward lengthening and shortening undoubtedly have played an important part in the geologic history[9] of streams. A well-known example is the gradual growth of Mississippi River from southern Illinois to the present Gulf of Mexico. A case of equal if not greater interest lies in the growth of streams which follow a sea retreating out over a rather uniform slope. The arrangement[10] of the main streams on the Piedmont Plateau suggests the hypothesis that they have evolved in much the same fashion as those on the Atlantic Coastal Plain whose growth taken algebraically has been mouthward incident to a receding shore line. Consequently, the coastal plain sediments,[11] of whatever thickness, may once have extended over much if not all the Piedmont Province. At least an analysis of the drainage in the large suggests such an hypothesis applied here, however, only to the streams of the Piedmont. The case of the Potomac and the Susquehanna where they cross the mountain and valley belts does not appear with equal clarity from the present study.

Mouthward elongation deserves to be ranked along with headward and it is only just in view of the facts to consider them of equal importance. This much may be ventured as a tentative opinion: that mouthward elongation of the trunk

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[8]Davis, W. M. Geographical Essays. Boston, 1909. P. 181. Grabau, A. W. Textbook of Geology. Boston, 1920. Part I, p. 712. Cotton, C. A. Geomorphology of New Zealand. Wellington, 1922. P. 70.

[9]Some recent publications of significant interest are:

Adams, George I. The course of the Tennessee River and the physiography of the southern Appalachian region. Journ. Geol., Vol. 36, 481–493. 1928.

Adams, George I. The streams of the coastal plain of Alabama and the Lafayette problem. Journ. Geol., Vol. 37, 193–203. 1929.

Flint, Richard Foster. Pleistocene terraces of the Lower Connecticut valley. Bull. Geol. Soc. Amer., Vol. 39, 980–981. 1928.

[10]See Chamberlin and Salisbury. Geology. New York, 1906. Vol. 1, p. 168, Fig. 160, or a drainage map of the United States. Also, Cotton, C. A. Geomorphology of New Zealand. Wellington, 1922. Pp. 69–70.

[11]Doctor D. W. Johnson, at the Toronto meetings of the Geological Society of America, December 30, 1930, presented the theory that the coastal plain sediments formerly may have extended 125 to 200 miles farther northwestward than they do now.

FIG. 9. Dendritic elongation and extension.

FIG. 10. A study in direction and pattern of elongation, showing mouthward and headward direction of lengthening as well as parallel and dendritic patterns.

FIG. 11. Elongation incomplete; elaboration scarcely started. Chiefly Wisconsin drift. Figs. 11–14 show the progress of elaboration.

FIG. 12. Elongation almost complete; elaboration started. Wisconsin drift.

portions of a drainage system has far more importance in the history of such a system than has headward elongation considered over a region and over a period of time.

Headward elongation is most aggressive where there is an optimum amount of slope and uniformity of surface. A surface like that on the Chokio quadrangle is inimical to steadily progressive and rapid headward growth. On the other hand, if the slope is too steep, headward growth apparently is retarded, as for example on the Allegheny ridges. The cause for the retardation lies among several factors such as thinness of soil, ground water surface, vegetation cover, nature of the rock, and the gradient of the run-off, all of which seemingly conspire to deliver the water in concentrated form at a comparatively low elevation on the mountain side. There must be some optimum slope and surface.

The subject of stream lengthening is complicated and perhaps merits more discussion than space permits. It is worthy of mention from the historical standpoint, however, that many streams undoubtedly have been lengthened headward following a waning ice sheet. An interesting study of stream growth in a mouthward direction may be made along shores as the waves recede and the tide goes out.

Elaboration of the System.—Elaboration refers to the constant development of minor tributaries which fill in the main body, or framework, of the growing system. The initially elongated system is expanded and embellished internally.

The Fargo map better than any other shows elongated streams with a minimum addition of tributaries. Elaboration may be followed as a progressive affair on the series of maps, Figures 11, 12, 13, 14, and 15, so chosen as to represent approximately the same relative positions with respect to the particular drainage systems. On the Waukee sheet the process of elaboration has just begun, whereas on the Melcher the branchwork of streams is fairly complex, most of the surface has been invaded, and the process therefore is approaching completion.

Elaboration eliminates the skeletonized form produced by elongation. The process constantly adds tributaries of decreasing rank until the branchwork, as a system of drainage, is fully elaborated. A system may be considered full-grown when it fulfills certain requirements discussed subsequently under the topic maximum extension.

FIG. 13. Elongation practically complete; elaboration well begun. Illinoian drift.

FIG. 14. Elongation done; fairly well elaborated. Illinoian drift.

FIG. 15. Elongation done; elaboration far along. Kansan drift.

FIG. 16. Territorial aggression. Stream A is the aggressor. Streams B, C, D, E, and F have been repressed. Stream F is submissive. Stage of extension.

Discussion.—Elongation and elaboration constitute the stage of extension; the two seldom can be separated save for mental convenience. Local elongation, however, must precede the addition of tributaries at any particular place. On the whole, lengthening applies equally as well to individual streams as to systems while elaboration can refer only to an entire system or a unit part of one. A stream or system once established must in the nature of things always continue its efforts to lengthen and expand, at least as long as the laws governing extension remain in operation. This apparently must be so, since extension is typified by the attempt to shorten the distance of rainwash travel. Competition arises not only among streams but also among drainage systems because of the inexorable desire to grow, and the satisfying of this desire carries the activities of extension, though not the stage itself, over into the stage of integration.

Perhaps the series of maps, Figures 11 to 15, deserves a further remark: the older drift sheets possess the more elaborate drainage systems, which alone would occasion no comment were it not for the fact that these particular maps were placed in sequence quite without forethought while a large number of maps were being analyzed and arranged in order. They were selected because of their closely similar positions in their respective drainage systems and only then were the particular drift sheets determined.

Pattern of Extension.—The patterns assumed by stream systems because of extension will be mentioned only in so far as a simplified analysis of the stage requires; the complete sequence of pattern development will not be considered. Maps such as shown on Figures 6, 7, and 8 illustrate parallel elongation, a very common type apparently if extension is in its early phases, or if the initial surface is of rather uniform nature and of definite slope, or if elongation occurs in a mouthward direction. (Of course the parallel pattern also develops under structural and lithologic control.) The influence of surface and slope becomes apparent in a study of the shoe string type of rills. The parallel arrangement develops gradually into a parallelo-dendritic pattern in absence of structural control and the original pattern may be restored in the main by blotting out the branchwork of tributaries fastened onto the mains.

The dendritic is the contrasted type of pattern which develops because of the nature of the surface, the regional

slope (or absence of it), and the materials. Figures 1, 2, 3, the north part of 4, and 5 show this type of extension on various surfaces. On figure 9 the dendritic pattern of lengthening applies equally well to different tributary groups.

Discussion.—A mention of dendritic pattern suggests the word "insequent" as used by Davis to[12] designate so-called self-guided streams, i.e., expanding stream systems controlled neither by initial slope, nor by difference of rock resistance, nor by structure.[13] Is this, however, a true lack of control even though the influence does not seem so definite as in the case of structurally controlled streams? In any case, insequent expresses a relation between surface and drainage and, though there is probably nothing fundamentally wrong with "insequent pattern," yet the word dendritic is much more generally used.

Although the dynamic viewpoint recognizes two fairly distinct types of pattern, the fact remains that variations and combinations of the two exist because of the influence of surface and material. Figure 10, illustrating not only both directions of elongation but also both patterns, furnishes a highly interesting study of surface form in relation to stream development from the short tributaries entering Lake Erie to the parallel streams in the southwest one-quarter of the map flowing down the back slope of a morainic ridge.[14]

Behavior of Streams During Extension.—A study of streams during extension reveals two contrasted types of behavior, *permissive* and *aggressive*. Permissive refers to the type whereby a stream or system extends into territory rightfully belonging to it in the course of natural development—that territory which it would be expected to occupy because of its position and relations. Each system develops normally in all its parts and drains a basin acquired by minimum encroachment on adjoining systems. Permissive behavior borders on the ideal since it requires fair play and an equitable distribution of territory, obviously a behavior calling for an unusual uniformity of surface, slope, material, and distribution of streams.

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[12]Davis, W. M. Geographical Essays. Boston, 1909. P. 174.

[13]For these controls see: Tarr and Martin. College Physiography. New York, 1920. P. 186. Grabau, A. W. Textbook of Geology. Boston, 1920. Part 1, p. 712. Lahee, F. H. Field Geology. New York, 1916. Pp. 336–339. Tarr and Martin say: "This insequent stream pattern is often treelike, for which reason the drainage is said to be dendritic."

[14]Leverett, Frank. Glacial formations and drainage features of the Erie and Ohio Basins. U. S. Geol. Survey, Mono. 41, plate 15. 1902.

The early phases of extension, to be sure, witness the permissive type of behavior to a much more perfect degree in the normal order of events than do the late phases. A study of ideal behavior has certain value for, if a drainage system is chosen at random and superimposed upon a chart showing the same system developed under ideally permissive behavior, any accidents, variations, or abnormal development may be detected. This can be done in very simple fashion with Figure 24.

Aggressive extension refers to the behavior by which foreign territory or neighboring streams are captured. Hence, there may be aggression (1) as to territory and (2) as to streams.

(1) On Figure 16 stream A has entered territory which belongs on general principles apparently to streams B, C, D, E, and F, and for that reason A is the aggressor. Streams B, C, D, and E have been repressed. Stream F is submissive because it has continued to grow, in a *different direction*, after repression. On figure 17, B, C, D, and E have been repressed by A. The principles governing aggressive and permissive extension will permit an interesting study of drainage behavior on the maps so far mentioned.

(2) Aggression with respect to streams is simply piracy as commonly understood. The type of piracy depends upon the impelling reason for the behavior; for instance, extension piracy has occurred on figure 18 at A. Since the larger streams crossing a barrier of resistant rock will cut down rapidly, tributaries to them will behave aggressively with respect to the smaller streams crossing the barrier and steal their headwaters. The smaller streams have been beheaded by the aggressive activities of the larger.

Discussion.—A realization that streams can be studied from the standpoint of behavior gives a clearer understanding of stream history in certain cases and a different method of approach to the study of land forms. Stream systems possessing obvious irregularities either have departed from a previous ideal scheme of development or are themselves more or less notable departures because of special initial, or inherited, conditions of the basin, and hence normal to those special conditions. Field observations should in most cases be the decisive criterion of differentiation. In any case, a concept of the ideal system and a knowledge of the variations will aid materially in deciphering the history of a system, in reconstructing the original surface, or both.

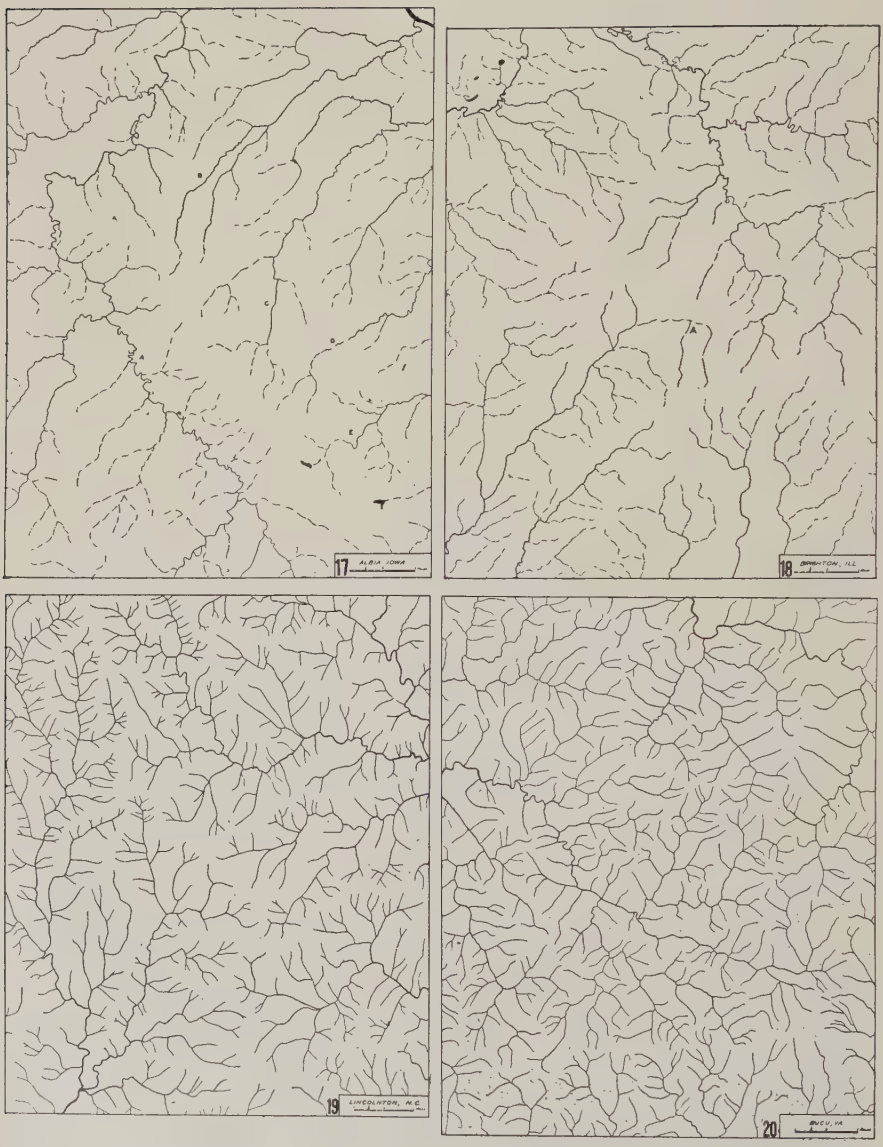

FIG. 17. Territorial aggression on a larger scale than on Fig. 16. Stream A, the aggressor, has repressed streams B, C, D, and E. Stage of extension.

FIG. 18. Aggression with respect to streams. Extension piracy has occurred at A. Extension well along.

FIG. 19. Maximum extension on the inner Piedmont Plateau. Coarse texture.

FIG. 20. Maximum extension on the Appalachian Plateau. Medium texture.

Although there are reasons for thinking that aggressive extension is a more normal affair than permissive, a knowledge of the latter facilitates an understanding of the methods, results, and relations of aggression. Very little if any aggression occurs during the initiation of a drainage system but it waxes greater as extension progresses and reaches a maximum as contiguous systems approach full development. Territorial aggression attains a maximum sooner than stream aggression.

Maximum Extension.—A system reaches maximum extension when elongation and elaboration have been completed—when the territory rightfully belonging to the system has been completely occupied. Active competition with contiguous systems, if such occurs, must therefore come for the most part after the attainment of maximum extension.

Figure 15 has the best developed drainage of any map among those so far given. Several varieties of maximum extension are shown on Figures 19, 20, 21, and 22, among which Figure 19 is slightly less well developed than the remaining three. The Lincolnton map is taken from a region of moderate relief on the inner Piedmont Plateau; the Bucu from a region of rather high relief on the Appalachian Plateau; the Prince Frederick from an area of low relief on the west shore of Chesapeake Bay; and the Ironton from an area of moderate relief near the west border of the Appalachian Plateau. The last two possess a fine texture.

Maximum extension is characterized by a lack of intermittent streams and by the presence of fully elaborated systems. It is first attained when the territory comes to be fully occupied by streams.

Discussion.—Extension is the stage wherein each system is impelled by the desire to shorten the distance of rainwash travel as much as possible by the lengthening of existing streams and by the addition of tributaries. In other words, extension is a process which attempts to increase the so-called drainage ratio until it reaches the maximum possible, that is, unity under ordinary circumstances, or a 45 degree slope. Exceptional slopes may, of course, be steeper. Nevertheless, this fixes mathematically and dynamically the time when maximum extension is attained at any locality, and an algebraic average applies to a system as a whole.

The query may arise as to whether any aggression either in respect to territory or to streams should be included within

FIG. 21. Maximum extension along west shore of Chesapeake Bay. Fine texture.

FIG. 22. Maximum extension at west border of Appalachian Plateau. Very fine texture.

FIG. 23. Maximum extension definitely past. The piracy at A, B, C, and D indicate that the systems had been fully extended prior to the present. Intermittency has returned.

FIG. 24. Early integration. Abstraction and absorption started.

the limits of the stage of extension. When a drainage system in a given region first and fully drains that region then the *stage* of extension has attained maximum. The climax of competitive aggression therefore occurs after the complete occupation of the drainage basin. Such a concept appears logical because of observation, because of its simplicity and utility, and because of the nature of the dynamic scheme. A map will serve as an illustration of the point. The piracy, as at A, B, C, and D, Figure 23, gives evidence that the territory had been completely occupied at some time in the past and for that reason the system is now post-maximum extension.

Maximum extension also represents the transition from extension to integration. At times maximum extension is a very brief interval; at others it is of considerable length. If the interval be long the dynamic cycle appears to include three stages rather than two. However, drainage systems considered dynamically pass through two distinct stages only—extension and integration—which account for practically all of the activities. Some activities may well occur after maximum extension is attained, but before integration becomes *evident.* The trunk areas of a system in a region of small drainage relief begin the processes of integration with little doubt long before the outlying parts of the system have finished extension.

No reference has yet been made to the change from intermittent to permanent streams during the progress of extension. If the maps are viewed in sequence it will be seen that intermittency disappears headward as extension progresses, that it is entirely absent at maximum extension, and that it reappears especially among tributaries with the progress of integration. This change of character, which is essentially a change of relationships, depends largely upon the depth, shape, and gradient of the ground water surface, the variation in the amount of run-off discharged to streams, and the depth of soil cover. During extension the ground water surface characteristically lies below the valley bottoms of many tributaries. All streams, however, apparently intersect the surface at maximum extension, a time when that surface possesses its steepest gradients and greatest local variations in altitude. With the progress of integration the ground water surface appears to be lowered and flattened. Decreasing rainfall incident to decreasing elevation in a region of initially high

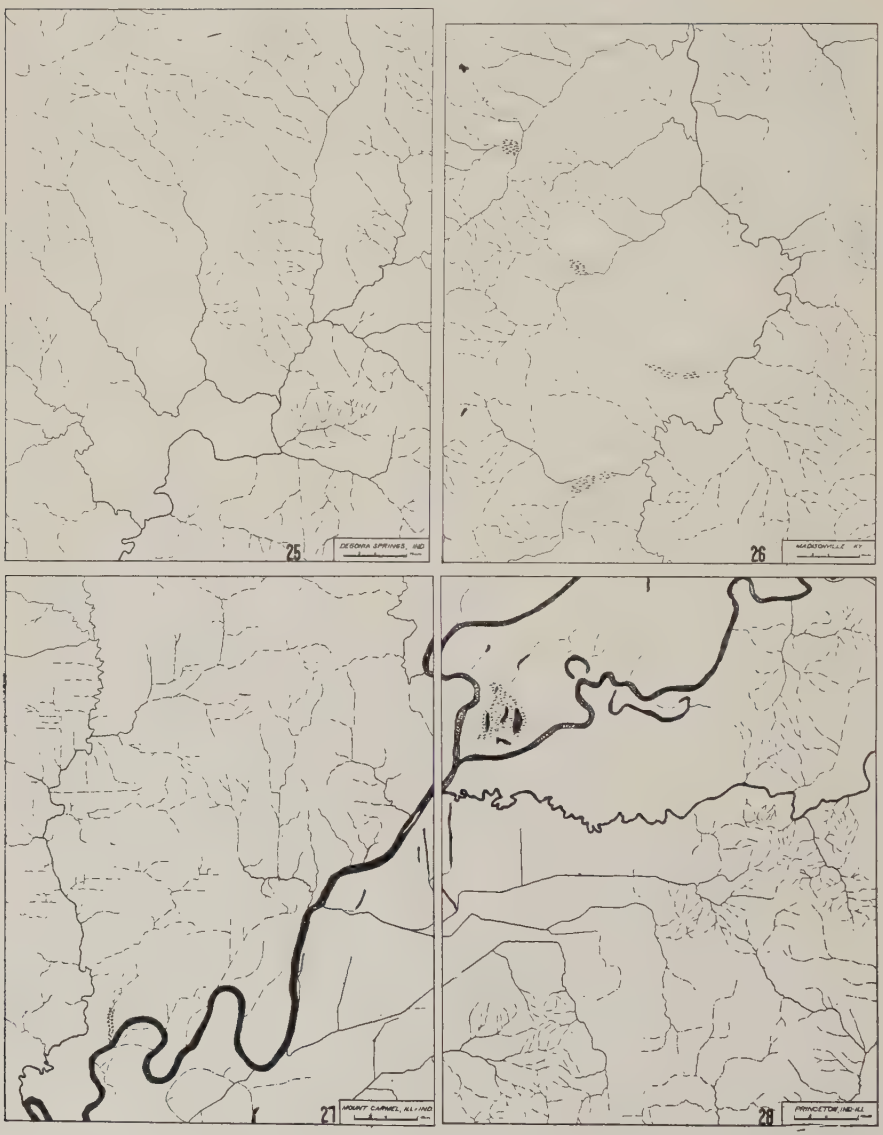

FIG. 25. Integration well started. The emergence of master tributaries.
FIG. 26. Integration rather far along. Abstraction quite evident.
FIG. 27. Rather advanced integration.
FIG. 28. Advanced integration. Master streams and master tributaries.

altitude undoubtedly is a factor[15] in the supply of ground water, but does not appear to apply in the case of the above-mentioned problem since the cycle of intermittency exists in regions of low as well as high elevation.

A study of the dynamic cycle has opened up a highly interesting problem on the relations between ground water and the history of the cycle.

INTEGRATION.

Extension is a time of increasing complexity, integration a time of simplification. The drainage system during integration maintains its control over acquired territory and at the same time consolidates its holdings, as it were, by a marked reduction in the number of tributaries, by the return of intermittent streams, and finally, by the emergence of master streams and master tributaries.

A thorough description and consideration of the detailed phases of integration are very much more difficult tasks than they are for extension because of the paucity of examples on present land surfaces. Some of the activities may be observed in a miniature fashion, but rarely on a large scale. The maps used as illustrations have been chosen to show the sequence of events to the best advantage for the size of the area.

The reappearance of the skeletonized form signalizes the definite existence of integration such as shown in Figure 24. Further progress of the stage appears on Figures 25, 26, 27, and 28, in a sequence which shows continued decrease in the number of streams, the spread of intermittency, and the gradual accentuation of the master tributaries. Figure 26 lies about intermediate in the progress of integration between Figures 24 and 25 and Figures 27 and 28. Of the series, the Princeton map (Figure 28) has progressed the furthest and it is of interest to notice that the Haubstadt map (Figure 24) which adjoins the Princeton on the south occupies a position somewhat more removed from the chief regional streams. The maps reproduced are fairly typical and represent, in rather brief fashion to be sure, several steps in integration. Maps from the lower Mississippi region show too small a section of the drainage system to be of comparative value.

The activities or processes responsible for the progress of integration appear to be abstraction, absorption, and a type of aggression.

[15]Davis, W. M. Geographical Essays. Boston, 1909. P. 262.

Abstraction.—Gilbert[16] defined the term as follows, "A stream which for any reason is able to corrade its bottom more rapidly than do its neighbors, expands its valley at their expense, and eventually 'abstracts' them." The idea is employed here in exactly the same sense save that the effects of lateral corrasion are also included.

Thus, abstraction is the elimination of tributaries, commonly of the shorter type, by the lateral and vertical migration of the main; it is also the loss of identity and personal independence of a secondary on the meander belt of the primary. The lateral migration constantly increases the immediate drainage area of the master itself at the expense of its tributaries. In this way, the lower part of a tributary system may be dismembered or a tributary may be distinctly shortened so that it ends at the base of the valley wall. An example, indefinite in the sense that it reverses the order of events, is shown on Figure 26 slightly northeast of the center. The main stream appears (on the topographic map) to lie sufficiently below the general valley bottom to permit the origin and growth of several small tributaries. Now, these tributaries in their recent formation illustrate, in reverse order, the elimination of just such streams by lateral swinging in the construction of a flood plain.

The elimination of streams because of vertical migration of the main, if such occurs, belongs properly to the stage of extension and therefore abstraction actually begins during extension but becomes neither predominant nor prominent in the sense here employed until after maximum extension has passed.

Absorption refers to the disappearance of streams permanently or partially probably because of a general flattening of the ground water surface and its consequent depression below the valley bottoms. The first step is the return to intermittency; the second, the complete elimination of the stream save during the immediate discharge of rainfall. Absorption is undoubtedly responsible not only for the disappearance of many small tributaries, but also for the return of intermittency in the whole headwaters area of a drainage system during the progress of integration.

Route to the Sea.—The attempt made by a master stream to secure the shortest valley route to the sea in harmony with

[16]Gilbert, G. K. Report on the geology of the Henry Mountains. U. S. Geog. and Geol. Survey of the Rocky Mtn. Region, Washington, 1877. P. 141.

the regional slope of a subdued or peneplain surface has been called aggression for want of a better name. Since the process depends upon stream activity and upon decreasing environmental control, it is classed under dynamic activities. The laws of flow are ultimately based on gravity and streams therefore desire the shortest route to their outlets, a desire the more nearly fulfilled as factors of environment, except regional slope, relinquish control.

Geological history probably must be called upon for examples. The Delaware, the Susquehanna, and the Potomac were true *integrational consequents* if they took approximately their present courses on a peneplain surface.

Results.—The net results of abstraction and absorption are the elimination of a host of tributaries from the plexus of streams in existence during maximum extension, the simultaneous accentuation of certain streams which finally emerge as master tributaries, and the production of a skeletonized framework just as typical in its way of late integration as the previous skeletal outline was of early extension.

RELATIONSHIPS.

The details in the development of a drainage system, especially those having to do with pattern and behavior, depend upon the nature of the surface, the slope, the material, and the structure. In the present work, adjustments to diverse structures and variable composition have not been considered. Uniformity of material and simplicity of structure have been assumed in order to keep the scheme as near the ideal as possible. The influence of those factors may then be treated as producing variations from the ideal, or simplified, scheme of development.

There is no intention to minimize the importance of land form or the influence of rock structure and lithology. Yet upon strict analysis, rock and structure may modify the valley form or the position of a stream but they can not alter the nature of the dynamic processes or the stream activities. The entire cycle as here outlined may even be considered to belong within the border-land connecting the active and passive phases of physiography. If so, the dynamic cycle has this distinctive feature: its origin is in the geodynamic rather than in the geomorphologic viewpoint.

However that may be, many features characteristic of the pattern of a drainage system depend clearly upon the influence of geologic environment. Stream adjustment is merely one example. A consideration of such environmental influences lies outside the province of the present paper; moreover they have been fully and admirably discussed by others.

FIG. 29. A summary diagram of the dynamic cycle: (1) initiation, (2) elongation, (3) elaboration, (4) maximum extension, (5) abstraction and absorption during integration, and (6) the emergence of master tributaries.

It will have been noticed that practically all of the illustrations have been taken from the humid portion of the United States. A drier climate undoubtedly would result in the following features in contrast with those described above: a great increase of intermittency; somewhat retarded elongation; poorly developed elaboration; a more skeletonized form at maximum extension; and an accentuation of the absorption process. On the whole the drainage system would be retarded in rate of development and would never attain the complex elaboration characteristic of a system under a humid climate.

Highly pervious rocks would have the same effect in some respects as a dry climate.

SUMMARY.

Figure 29 is an ideal summary of the dynamic cycle.

Classification is a matter of convenience, an expedient permitting us in many instances to grasp certain concepts and to transfer them to others. The drainage cycle actually knows no distinct subdivisions, although it does divide itself into general stages governed by certain prominent characteristics. Phases akin to extension may extend far into integration; and integration may begin its activities locally early in extension. The drainage system taken throughout its cyclic history reveals no sharp boundaries, no lines of cleavage where one set of characteristics ends and another begins. Only a preponderance of process or activity justifies the privilege of classification.

The dynamic cycle includes the history of a drainage system from initiation through the stages of extension and integration, or to the event whereby initiation begins anew. Strictly, the dynamic cycle refers to a series of events repeated cyclically and characterized by two sets of activities of which one set dominates extension and the other dominates integration. Diastrophism not only motivates the cycle but also initiates or interrupts it. Climate apparently regulates the intensity of the extensional activities, elongation and especially elaboration. The relations between climate and ground water must bear directly upon the very nature of the cycle itself. If so, several interesting problems await solution.

At the beginning of extension initial streams are elongated and the system is elaborated by the addition of tributaries of constantly decreasing importance until the fully developed branch-work occupies the basin blocked out originally by the elongated streams when they first made drainage contact with adjoining systems. Abbreviated streams and the skeletonized form have disappeared at maximum extension which, expressed more precisely, is attained when the so-called drainage ratio reaches a maximum. Intermittency has at the same time decreased to zero.

Integration in a measure reverses the processes of extension, for abstraction and absorption eliminate tributaries until merely a skeletonized framework remains to care for drainage.

Intermittency returns and spreads progressively among the tributaries. During the final phases of integration so far recognized emphasis is placed upon certain members of the system whereby master tributaries come to dominate the ultimate skeletal system, and the trunk stream seeks the shortest valley route to a point of discharge consistent with regional slope. The cycle may then be repeated or else terminated in accordance with subsequent diastrophism.

Extension is a time of conquest and minute invasion; integration a time of withdrawal and consolidation. In the whole story the rôle of climate, ground water, the drainage-ratio factor, and their mutual relationships appear to be of paramount importance in the evolution of the dynamic cycle.

THE EPIBRANCHIAL GANGLION OF THE GLOSSOPHARYNGEAL NERVE IN AMBLYSTOMA JEFFERSONIANUM.

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INTRODUCTION.

The epibranchial placode of the glossopharyngeal nerve in *Amblystoma jeffersonianum* has many characteristics in common with that of the facial nerve, but differs in the relation of the placode to the endoderm of the pharyngeal pouch. The second or glossopharyngeal pouch forms an open gill slit while that on the first or facial pouch does not become patent and withdraws from the ectoderm, leaving a detached mass of endoderm which later disappears. As a result of the presence of a permanent contact between the endoderm of the pharyngeal pouch with the ectoderm which forms the branchial cleft, the epibranchial placode of the glossopharyngeal nerve remains for a long time in contact with the endoderm and becomes detached relatively late while the placode of the facial nerve becomes detached from the endoderm relatively early.

The origin of the placodes of both nerves furnish very definite and positive evidence of the derivation of the placode from ectoderm from which the placode later, after a growth period, becomes detached from the ectoderm, moves medially and rests on the dorsal surface of the endoderm of the pharyngeal pouch. After this migration it joins the remainder of the glossopharyngeal ganglion derived from the neural crest and from the lateralis placodes. It is not possible in the case of either ganglion to follow the epibranchial placode after the fusion of the placode with the remainder of the ganglion occurs, until the differentiation of the definitive ganglion cells takes place. Kostir (24) has done this for the 11.5 mm. embryo and the description of the more difficult stages to analyze follows his description.

Stone (22) has shown that the removal of the neural crest does not prevent the formation of the placodal ganglia and that the removal of the ectodermal placodes does prevent the formation of the placodal ganglia. In contrast to the

experimental and embryological evidence derived from the urodeles, Adelman ('25) holds that in the white rat the placode arises as the result of the stimulus furnished by the neural crest and G. Elliot Smith ('28) quotes Hill to the effect that in echidna the placodes arise from the endoderm. Whatever value comparatively the evidence from fishes and urodeles may have it is positively against the theory that the epibranchial placodes arise as a result of the stimulus of the neural crest or that the placodes are endodermal in origin.

The author, Landacre ('10), has previously cited the evidence for the function of the epibranchial placode after joining the remainder of the cranial ganglia. It is briefly as follows: every nerve having gustatory fibers has an epibranchial ganglion; no nerve without an epibranchial ganglion has gustatory fibers; the size of the epibranchial ganglion is always proportional to the size of the epibranchial placode; in Ameiurus, which has an enormous epibranchial placode on the glossopharyngeal nerve and a small easily followed lateralis component and no recognizable neural crest component, the nerve is apparently aside from the lateralis component exclusively gustatory.

The differentiation of structures derived from neural crest or from ectoderm as compared with those derived from endoderm is relatively easy in the urodeles owing to differences in size of cells and in the number and size of yolk granules. Endoderm cells and structures derived from endoderm consist of large cells and contain numerous large yolk granules which stained with Delafield and orange G give a light yellow field with few nuclei. If stained with iron alum, such a field is dense black. Cells and structures derived from ectoderm and neural crest consist of smaller cells with small yolk granules presenting a darker denser mass when stained with Delafield and orange G. The distinction based on yolk granules exists even in mesenchyme, so that the two types of cells can be recognized even where they mingle in early embryos.

One of the striking features of the history of placodes in urodeles is the fact that the placodes grow as solid masses of ectoderm and become detached from the ectoderm as masses which are relatively easy to follow during the migration medially and during the time the placode rests on the endoderm of the pharynx. The distinction between ectodermal and endodermal derivatives persists until the absorption of yolk granules occurs, which is far beyond stages involved in the present problem.

MATERIAL.

The material consists of stages 26 to 45 of *Amblystoma jeffersonianum*. Sections were cut transversely 10 micra thick, stained in Delafield's hematoxylin and counterstained in orange G.

TABLE SHOWING AGE AND AGE INCREMENT OF STAGES INVOLVING EPIBRANCHIAL PLACODE IX.

No. of series.....	26	27	28	29	30	31	32	33	34	35
Age in hours.....	238	243	249	255	261	267	273	280	287½	292
Increment.....	5 h	5 h	6 h	6 h	6 h	6 h	6 h	7 h	7½ h	4½ h
No. of series.....	36	37	38	39	40	41	42	43	44	45
Age in hours.....	297	302	308½	312	316	320	324	329	334	338
Increment.....	5 h	5 h	6½ h	3½ h	4 h	4 h	4 h	5 h	5 h	4 h

The history of the epibranchial placode on IX falls into two rather definite periods. The first period covers the time of growth of the placode in the nervous layer of the ectoderm and the second period the time during which the placode after completing its growth rests on the endoderm of the pharyngeal pouch during which the placode also becomes more or less completely fused with the remainder of the glossopharyngeal ganglion. This ganglion in Amblystoma has in addition to the contribution from the epibranchial placode definite contributions from the neural crest and from the dorsolateral placode.

The diagonal position of the ninth ganglion in Amblystoma makes it impossible in transverse sections to show except occasionally the fusion of the placode with the remainder of the ninth ganglion. This condition is in striking contrast to the condition of the facial ganglion. There is another rather striking difference due to the persistence of the pharyngeal pouch. The placodal portion of the IX ganglion remains in contact, resting on the dorsal surface of the pouch for a relative long period compared with the behavior of the placode of VII.

THE EARLY GROWTH PERIOD.

The early growth period is illustrated in Figures 1–4, inclusive. Figure 1, taken from series 26, is ten hours older than the first series in which the epibranchial thickening occurs, but is the earliest series in which there is marked evidence of growth as indicated by definite thickening of the primitive line. In stage 24, nine days and twelve hours after deposition,

3.75 millimeters in length and with twelve somites, the primitive thickening can be recognized,

After the epibranchial placode begins to grow there is a steady increase in its thickness and in its extension medially as a triangular solid mass. This epibranchial mass which arises from the nervous layer of the ectoderm rests with its base on the ectoderm and its apex directed medially. In the first section figured (Fig. 1, right side) it is not possible to separate the placodal thickening into epibranchial and dorsolateral because of the fusion of the two. The ventral portion of the placode on right side is epibranchial and the dorsal portion is dorsolateral and gives rise to the lateral line placode. In older stages this distinction can be made since the lateralis ganglion placode lies slightly caudal to the epibranchial placode, while the lateral line placode lies dorsal at least to the caudal portion of the epibranchial placode.

Part of the difficulty of separating the epibranchial and dorsolateral placodes is illustrated by a comparison of the right and left sides of Figure 2, where the section passes through the rostral portion of the placode on the right side and through the middle of the placode on the left side. The epibranchial placode of IX is situated well dorsal on the side of the body resulting in more or less fusion between epibranchial and dorsolateral placodes. The right side of Figure 2 illustrates also the presence of the placode rostral to the junction of the pharyngeal pouch with the ectoderm. The dorsal position of the epibranchial placode is illustrated in Figure 3. Here the section passes through the middle of the placode on both sides.

In Figure 4 the distinction between epibranchial placode and the lateral line placode is readily made. The lateral line placode lies dorsal to the epibranchial placode on the right side, while the lateralis ganglion is caudal to the level of this section. In the same figure the extension of the epibranchial placode medially is evident on right side. Both sides show the closeness of contact between the placode and the endoderm. The placode becomes detached from the nervous layer of the ectoderm except at its ventral border before any marked migration medially occurs.

During the growth period up to the time of complete detachment of the placode from the ectoderm it is evident that the placode is ectodermal in origin, that part of the placode lies rostral to the contact of the pharyngeal pouch with the

ectoderm and that the whole placode lies rostral to the neural crest portion of the IX ganglion.

THE PERIOD OF CONTACT WITH ENDODERM AND FUSION WITH THE REMAINDER OF VII.

During the second period the epibranchial placode becomes detached from the lateral ectoderm except at its caudal border where the truncus glossopharyngeus arises. At this level the epibranchial placode is continuous with the ectodermal mesenchyme lying ventral to it. This contact is similar to that in similar stages of the facial placode. As illustrated in Figure 5, the junction of the placode with the pharyngeal pouch is at the lateral border of the pouch. In later stages the placode comes to rest on the dorsal border of the endodermal pouch. The placode in Figure 5 is not completely detached from the ectoderm, at least a small group of cells lies between the two and in contact with both.

Figure 6 illustrates a constant condition in the relation of the placode to the lateral border of the pharyngeal pouch. The placode bifurcates over the lateral portion of the endodermal pouch and the medial portion of the placode seems to give rise to a ramus pharyngeus while the lateral portion later sends fibers into the truncus glossopharyngeus. This bifurcation is constant in all early series, but when the seventh ganglion becomes detached from the pharynx and lies more dorsal in the body the diagonal course of the pharyngeal ramus makes it difficult to follow.

In stage 39, Figure 7, the change in condition of the placode is slight, showing only a slight detachment from the pharyngeal pouch. Figures 8 and 9 from the same embryo are presented to show the differentiation into neural crest and lateralis portions of the ganglion. The cellular contact of the lateralis portion of IX with the ectoderm illustrated in Figure 9, right side, is interesting since it seems to persist in Amblystoma from the time the placode arises from the ectoderm.

In stage 42 (Fig. 10) the placode is detached from the endoderm of pharynx, but a few sections rostral rests definitely on the endoderm and further shows the bifurcated condition mentioned above. The placodal portion of the ganglion withdraws from the endoderm from caudal to rostral.

The bifurcated condition of the rostral portion of epibranchial IX is shown in Figure 11, right side, where the origin

of both ramus pharyngeus and truncus glossopharyngeus can be observed. In this stage the rostral portion of neural crest IX rests on dorsal surface of placodal IX. The age at which the epibranchial portion of IX ceases to rest on the pharyngeal pouch in contact with the endoderm varies. In a series four hours younger than stage 45 (Fig. 12) the rostral portion of IX, which is composed exclusively of cells derived from the epibranchial placode, lies well dorsal and has withdrawn completely from the pharynx. In two series four and one-half hours older than 45 (Fig. 12) the epibranchial placode touches the endoderm throughout the extent of a few cells.

Figure 12, right side, illustrates the last stage in which there is a well defined contact between the placodal ganglion and the endoderm. The placode is massive and the small group of cells resting on the dorsal surface of the placodal ganglion illustrate the plan of junction between the cells from the two sources. Either the neural crest cells shift rostral onto the dorsal surface of the placodal cells or the placode shifts caudal ventral to the neural crest cells.

SUMMARY.

The origin of the epibranchial ganglion of the glossopharyngeal nerve resembles closely that of the facial nerve. Each epibranchial placode is preceded by a primitive line which can be identified prior to the actual growth period in the formation of the placode. The growth period begins with a definite increase in the thickness of the placode which forms in the nervous layer of the ectoderm. This thickening lies in part rostral to the endodermal pharyngeal pouch and entirely rostral to the neural crest portion of IX. The epibranchial placode of IX begins its definite growth phase simultaneously with that of the dorsolateral placode which is continuous on its rostral border with the lateral line placode. The lateral line placode and the lateralis ganglion placode however have a more dorsal position than the epibranchial placode. In the earliest stages of the growth of all three structures there is some difficulty in separating them. This difficulty disappears when the three placodes assume definite histological structures.

The epibranchial placode during the growth period appears as a solid mass of cells, triangular in form with the base of the triangle resting on the ectoderm and with its apex directed medially. As the placode increases in size its medial portion

abuts against the lateral extension of the pharyngeal pouch and does not as in the case of VII come to rest at first on the dorsal border of the pharyngeal pouch. In later stages the placode loses its triangular form and consists of a rounded mass of cells which at its rostral end bifurcates over the lateral border of the pharyngeal pouch the medial arm of the ventral bifurcation seeming to give rise to a pharyngeal ramus and the lateral arm enters the truncus glossopharyngeus.

The caudal border of the epibranchial placode abuts at first against the neural crest portion of IX but in later stages there is a change in this relation and the neural crest portion of IX at its rostral border comes to rest on the dorsal border of the epibranchial portion. In still later stages the whole combination of IX withdraws dorsally and the ganglion is detached completely from the pharyngeal pouch. Since the epibranchial ganglion of IX arises entirely rostral to the neural crest the neural crest could not be considered as a stimulus to the formation of the epibranchial placode.

The differences in histological detail between ectodermal derivatives with their small cells and small yolk granules and the endodermal cells with their large size and large yolk granules leaves no doubt as to the ectodermal source of the epibranchial placode. This conclusion is further strengthened by the growth of the placode in the nervous layer of the ectoderm and by its compactness, since it is rare to find the borders of the placode irregular, and the gradual migration medially prior to its junction with the neural crest and dorsolateral portions of IX. The evidence points to the conclusion that the epibranchial placode is a ganglion forming structure, not dependent on the neural crest or even the pharyngeal pouch for stimulation and not a phylogenetically old sense organ and definitely ectodermal in origin like all other ganglia.

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ABBREVIATIONS USED.

L. P.—Lateral line placode.
E. P.—Epibranchial placode.
A. V.—Auditory vesicle.
N. C. G.—Neural crest portion of ganglion.
L. G.—Lateralis portion of IXth ganglion.
R. IX—Root of IX.
E. G.—Epibranchial portion of IXth ganglion.
G. IX—Glossopharyngeal ganglion.

DESCRIPTION OF PLATES.

All figures are untouched photographs of transverse sections 10 micra thick of *Amblystoma jeffersonianum*. Sections were stained in Delafield's hematoxylin and orange G and photographed at a magnification of ×75 and reduced to ×35 for printing.

Plate I.

Figures 1–4, inclusive, cover the growth period of the placode in the nervous layer of the ectoderm.

Fig. 1. Series 26, Section 123, right side rostral to left. Section or right side in middle of placode which is ten sections long. The caudal tip of the auditory vesicle and the root of the IX nerve on right side. Neural crest portion of IX on left side of section. Lateral line placode on dorsal surface of epibranchial placode on right side.

Fig. 2. Series 28, Section 120, right side slightly rostral to left. Left side through middle of placode. Right side through rostral portion of placode which here extends three sections rostral to the contact of pharyngeal pouch with the ectoderm and is fused on its dorsal surface with the primordium of the lateral line placode.

Fig. 3. Series 29, Section 132, right and left sides symmetrical and at the middle of the epibranchial placodes. Epibranchial placodes in Figures 1, 2, and 3 lie at same dorsoventral level as the lateralis ganglion placodes which are located more caudal. These two placodes do not appear in the same transverse section of the IXth ganglion as they do in the case of the VIIth ganglion.

Fig. 4. Series 32, Section 165, right side slightly caudal to left. Epibranchial placode on right side taken through middle of placode which is twelve sections long. Compared with Figure 3 the placode on the right side has grown medially but is still attached to ectoderm. On left side placode extends ventrally continuous with nervous layer of ectoderm. Lateral line placode appears on right side dorsal to and in contact with the epibranchial placode.

Figs. 5–12, inclusive, cover the period of contact with the endoderm and fusion with the remainder of IX.

Fig. 5. Series 35, Section 152, right side caudal to left. Epibranchial placode eight sections long. Right side through middle of placode which is detached from ectoderm except for a small group of cells still lying between placode and ectoderm. Placode closely attached to lateral border of pharyngeal pouch. Lateral line placode on right side.

Fig. 6. Series 38, Section 150, right side slightly caudal to left. Placode which is seven sections long free on right side from IX. Two sections caudal to right side placode is fused with IX. Placode on right side rests definitely on pharyngeal pouch. On left side, which is slightly rostral to right, and two sections from rostral end of placode, the placode shows the typical bifurcation of placode over the lateral border of pharyngeal pouch.

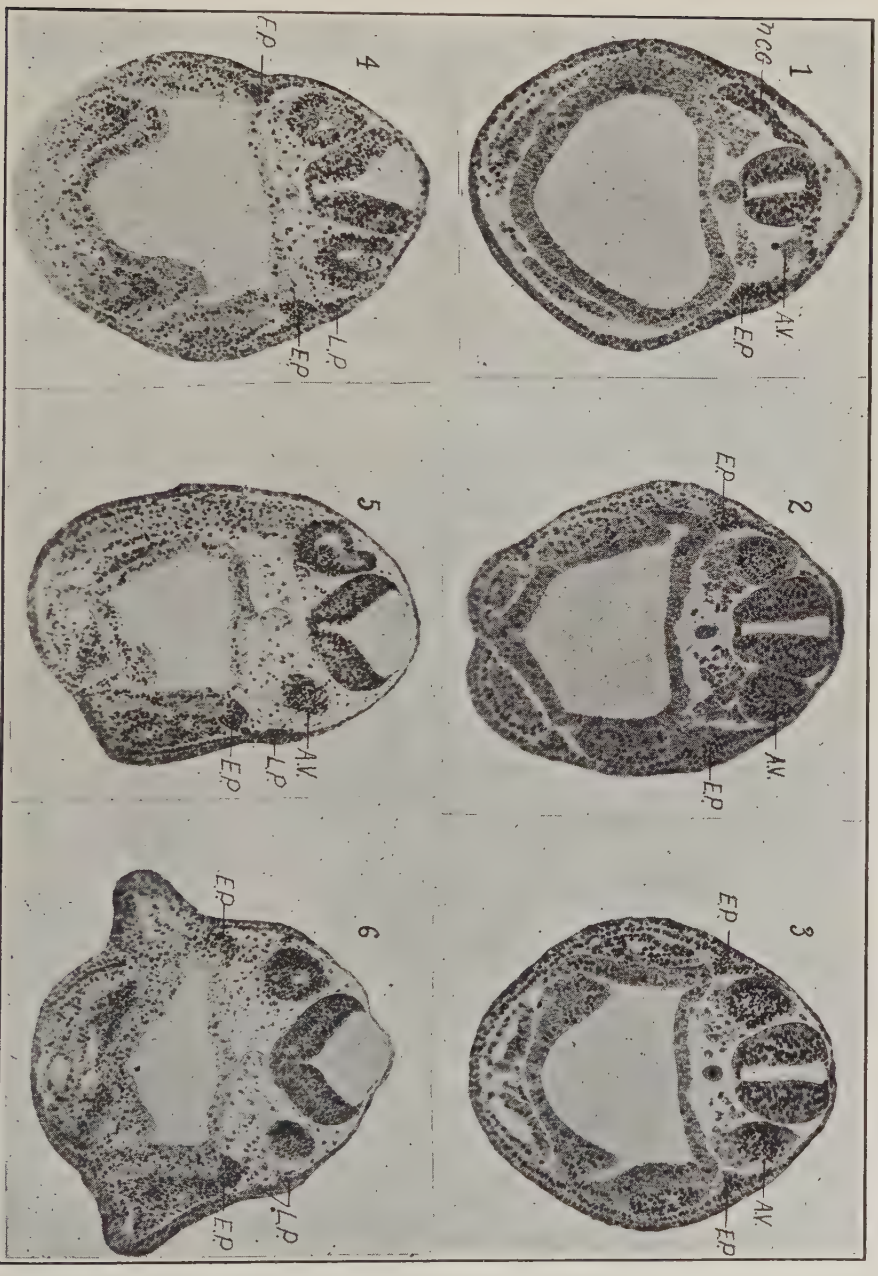

1
n.c.c.
A.V.
E.P.
2
E.P.
A.V.
E.P.
3
E.P.
A.V.
E.P.
4
E.P.
L.P.
E.P.
5
A.V.
L.P.
E.P.
6
E.P.
L.P.
E.P.

Plate II.

Fig. 7. Series 39, Section 169, right side rostral to left. Free portion of placode on right side six sections long. Figure 7 is taken through the fifth section of placode on right side, on left side section passes through the junction of the placodal and neural crest portions of IX. The placodal portion of the ganglion lies medial to neural crest portion. The placode on right side still rests on pharyngeal pouch, but the line of contact between placode and endoderm is reduced and at the lateral border of the placode the placode is becoming detached.

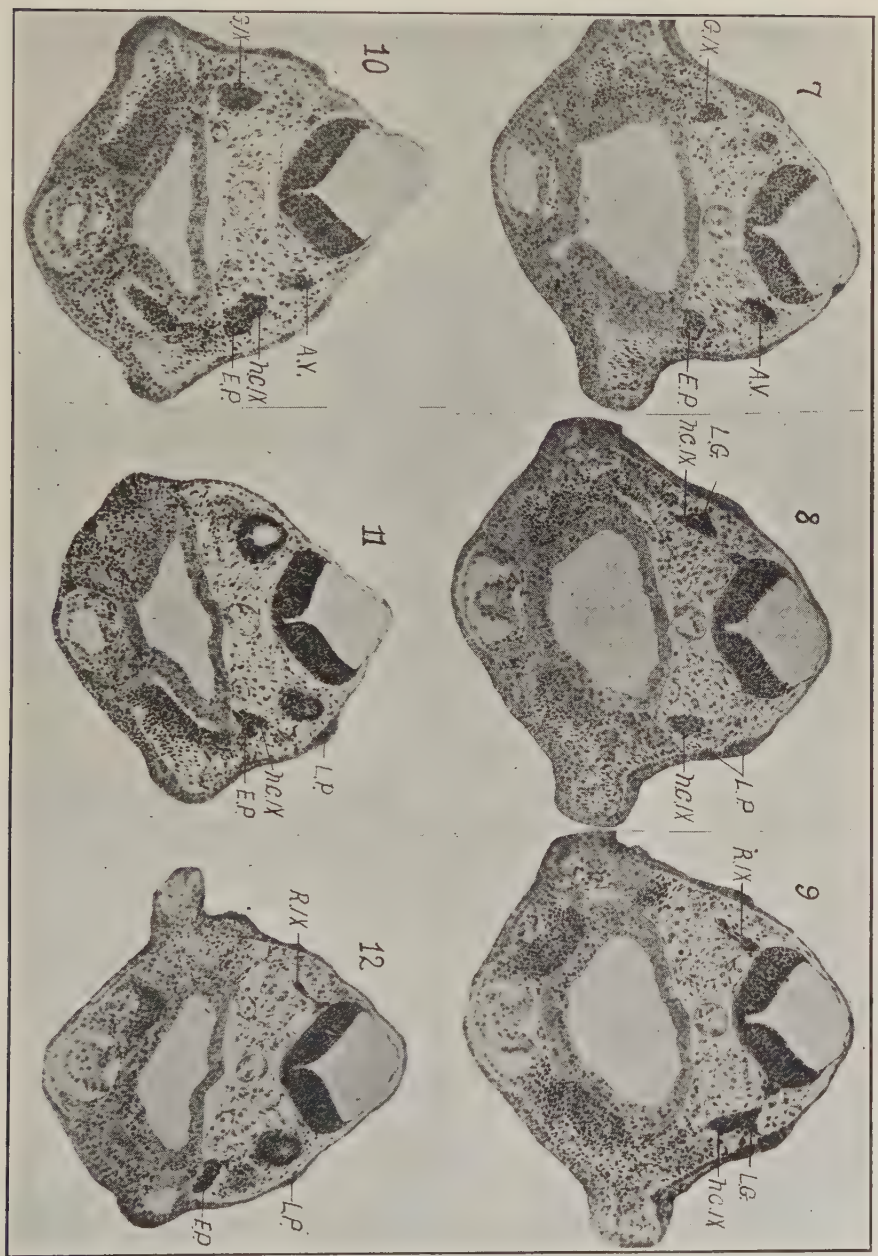
Fig. 8. Series 39, Section 175. On right side section passes through the neural crest portion of IX anterior to the junction of neural crest and epibranchial portions. On left side section passes through the root of IX and the combined neural crest situated medially and lateralis portions of IX situated laterally.

Fig. 9. Series 39, Section 178. On right side section passes through the root of IX, the lateralis ganglion of IX situated dorsally and laterally, and the neural crest portion of IX situated ventrally. The lateral portion of the ganglion consists of lateralis IX from which arise the cellular rami. The more dorsal ramus is ramus auricularis IX and the more ventral ramus is ramus supratemporalis IX. The right side of this figure illustrates a characteristic condition of the early cellular composition of lateral line nerves. On left side the section passes through the root of IX.

Fig. 10. Series 42, Section 166, right side rostral to left. Right side passes through the combined epibranchial and neural crest portions of IX, the epibranchial placode lying more ventral and lateral to the neural crest portion. The lateralis ganglion is caudal to this section. On left side of section epibranchial and neural crest portions are closely fused. On right side the close relation of the ganglion with the ectodermal mesenchyme lying ventral to the ganglion is evident. At this level the truncus glossopharyngeus arises. The detachment of the epibranchial placode from the pharyngeal pouch at this level is evident.

Fig. 11. Series 43, Section 160, right side caudal to left. IXth ganglion on right side, three sections from rostral end, consists of the epibranchial ganglion bifurcated over the pharyngeal pouch and the neural crest portion lying dorsal to epibranchial portion. The lateral portion of the epibranchial ganglion lies at the level of the truncus glossopharyngeus and the medial portion gives rise to a small nerve that is apparently the ramus pharyngeus IX. On right side only a few cells of neural crest IX rest on epibranchial IX.

Fig. 12. Series 45, Section 166, right side rostral to left. On right side the section passes one section rostral to truncus glossopharyngeus and three sections from rostral end of ganglion IX. The placodal ganglion is here very compact and readily distinguished from endoderm of pharyngeal pouch. This is the last stage where there is a constant contact between epibranchial IX and the endoderm of pharyngeal pouch.


7
G.IX
A.V.
E.P
hc IX
8
L.G.
hc IX
L.P
9
R.IX
L.G.
hc IX
10
G.IX
A.V.
hc IX
E.P
11
L.P.
hc IX
E.P
12
R.IX
L.P.
E.P

CHARACTERISTIC EXAMPLES OF ACCUMULATIVE PROGRESSIVE EVOLUTIONARY MOVEMENTS.*

Studies in Determinate Evolution, V.

JOHN H. SCHAFFNER.

The proper way to study evolutionary movements is to follow out the changes which occur in the activity of particular potentialities, and it is evident that a proper phyletic taxonomy can result only when the entire complex of hereditary potentialities possessed by the cell and expressed as characters in the individual is taken into consideration. Furthermore, the addition of potentialities step by step in a definite progression is one of the very striking manifestations of the evolutionary process by which comparative levels may be determined. In the present paper, studies of five prominent series of this nature are outlined. The first four deal with progressions within rather narrow limits and are confined in each case to a single genus, while the last one takes in a somewhat wider range, extending from the lowest living member of one order to the culmination species of one line of the next higher order in the phylogenetic relationship.

THE GENUS LYCOPODIUM.

There are several phyletic lines in the living species of *Lycopodium*. Taking representatives of our common northern species from the simplest to the most complex, we obtain the following progressive series:

1, *Lycopodium lucidulum;* 2, *L. alopecuroides;* 3, *L. annotinum;* 4, *L. clavatum;* 5, *L. obscurum;* 6, *L. complanatum;* 7, *L. tristachyum.*

In the lowest species, *Lycopodium lucidulum*, there is no determinate reproductive axis, the zones of sporophylls simply alternating with the zones of foliage leaves. There is no difference in the response of the various buds, all growing in one direction against the force of gravity and the direction of light. There is practically no dimorphism of the leaves and the leaves have practically no phototropic reaction, not being

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able to adjust themselves even out of the shade of their own stems. The growth of the stem is comparatively slow and about the same in all the buds. The dichotomous division of the buds is also comparatively slow. As one goes upward through the series of species there is almost a uniformly progressive building up of a more complex reaction system. Each new acquisition is carried through to the end of the series and is often decidedly improved. In *Lycopodium alopecuroides* a determinate condition is established with the reproductive process, which gives rise to a poorly differentiated cone. There is also some slight difference between sporophylls and leaves. A differentiated growth potentiality is introduced so that one branch of a dichotomy grows faster than the other. The slow-growing branch is the determinate reproductive branch which grows erect while the second branch of the dichotomy is a more rapidly growing, more flexible vegetative and indeterminate branch. Although the vegetative branch grows upwards it is finally brought to the ground because of its flexibility and takes root at the point of contact from which the growth and reaction continue as before.

In *Lycopodium annotinum* the differentiation between the branches of the primary dichotomies is far advanced. One branch is creeping, grows rapidly at right angles to gravity and the substratum while the other grows erect and often divides several times. All the axes of the erect branches show a definite determinate growth, some ending in cones and some stopping growth permanently in the vegetative condition, while the horizontal branch grows indefinitely. There is a very decided dimorphism between the sporophyll and foliage leaf but no peduncle is developed, the transition being directly from foliage leaf to sporophyll at the base of the cone. Thus three great properties are established which are characteristic of most of the highest plants, namely, reproductive and vegetative determinate axes and differentiation of foliage leaves and sporophylls.

In the fourth stage, represented by *Lycopodium clavatum*, efficiency of the growing system of the creeping branch is increased decidedly and the erect reproductive shoot becomes more of a unit. But the greatest advance is a disturbance established between the vegetative part and the cone, a very prominent peduncle being produced with highly specialized reduced leaves. This peduncle usually divides once giving

rise to the most primitive type of inflorescence, a cluster with two flowers. The disturbance between the flower and the vegetative system below is a nearly universal characteristic of all higher plants. It is one of the important progressive movements and in *L. clavatum* we have one of its first appearances. The plant now has three distinct types of leaves without taking account of the specialization of the leaves on the creeping rhizome, due probably to a special environment in the surface of the substratum.

In *Lycopodium obscurum* (No. 5) the aerial branching system becomes much more complicated and the leaves on the determinate vegetative branches begin to show a decided reaction to light during their development. To a small extent also the branches show a definite reaction and are beginning to spread out into imperfect fan-shaped systems. In practically all lines, *L. obscurum* is an advance over *L. clavatum* except that it has not evolved a peduncle. Occasionally even in a very definite orthogenetic series a certain member may retain a primitive condition while most of its other important characters are evolving in a regular forward progression.

All of the progressive movements and complexities so far established in the series are carried forward in *Lycopodium complanatum*. The rhizome is very long and has a rapid growth; the branching system of the erect stem is decidedly more complex; and the dichotomy in the peduncle is increased so that each peduncle usually bears from four to eight cones. The determinate vegetative branches are decidedly flattened and dorsiventral with differentiated upper and lower surfaces and form definite fan-shaped systems spread out to the light because of the acquirement of a complex reaction, responding to light and gravity in a definitely correlated manner. The leaves on the flat branchlets are of three types; the two lateral rows are broad and alike, while the upper and lower rows are narrow and also differ from each other. This development of flattened fan-like systems of branches is repeated many times and becomes especially prominent in certain groups of conifers. Species with fan-like branches are especially abundant in *Selaginella* and *Thuja*. The progression in the reaction system to gravity and light and also in the morphological expression is very evident in this series. In *L. lucidulum* there is but one reaction for all buds; in *L. alopecuroides* there are two reactions but they are not very perfectly differentiated;

in *L. annotinum* there are two definite reactions; in *L. obscurum* there are three; and in *L. complanatum* there are also three reactions, but they are more complete or extreme than in *L. obscurum*.

Lycopodium tristachyum is a little more extremely developed along the same lines as *L. complanatum*, except that the branchlets appear less flattened because they are narrower and the leaves more reduced. There is greater branching potentiality in the aerial shoots so the peduncles commonly have 8 or more cones instead of 4–6. The vegetative branches composing the fans are also more numerous and the horizontal stems are extensively creeping, 1–4 in. below the surface. There are seven distinct types of leaves on the plant the same as on *L. complanatum*.

Lycopodium complanatum and *L. tristachyum* compared with *L. lucidulum* show, among other characters which might be considered, the following ten important lines of cumulative, evolutionary advancement:

1. From indeterminate growth for all axes to determinate growth of the reproductive branches in addition to the indeterminate growth of the creeping axis.
2. From no definite dimorphism of the foliage leaves and sporophylls to a decided dimorphism with highly differentiated sporophylls.
3. The origin of definite determinate growth in the vegetative aerial branches.
4. Evolution to a dorsiventral shoot system, involving leaves and stems and giving a definite reaction to light, the upper side being darker green than the lower side.
5. Differentiation of the leaves has taken place, so that, counting the sporophylls, there are seven distinct types of leaves instead of the uniform type of *L. lucidulum*.
6. Development of a very rapidly growing and extensive rhizome.
7. Differentiation of response to gravity and light has been introduced so that at each primary dichotomy of the indeterminate horizontal axis one of the twin buds grows at right angles to the force of gravity and the other grows upward against it.
8. Development of a branching system in the reproductive shoot giving rise to an inflorescence.
9. Development of a peculiar type of hereditary expression between the flower and the vegetative axis below, giving rise to a prominent peduncle.
10. Great development and improvement in the vegetative branching system through the presence of a more rapid dichotomy of the growing bud of the aerial shoot.

The development of flowers, differentiated sporophylls, peduncles, and inflorescences, through branching activity expressed in the reproductive shoot, are all decidedly characteristic of the higher plants. The change from a simple vegetative geotropic response to a complex reaction to gravity of various vegetative points of the stem system is also repeated in a multitude of cases in the higher plants. The reaction is to a condition universally possible to all and since only a part took the step, the cause is not to be looked for in the presence of the ground environment beneath nor to the influence of gravity, which acts equally all over the earth, but in the ultimate constitution of the structure of the living systems involved.

THE GENUS EQUISETUM.

The genus *Equisetum* represents a survival of a single small group of a phylum that in ancient geological times had an abundant and complex development. *Equisetum* is both primitive and at the same time highly specialized. The living species form a system of quite closely related groups which show a remarkably consistent progression from the lowest stage to the very highest. Disregarding the segregative characters and various repetitions which appear at the culmination points of the six main sections into which the genus falls, the complete progressive accumulation of the important characters can be represented by the following series:

1, *Equisetum giganteum;* 2, *E. myriochaetum;* 3, *E. ramosissimum;* 4, *E. laevigatum;* 5, *E. fluviatile;* 6, *E. silvaticum;* 7, *E. arvense.*

Equisetum giganteum is a plant with a long-lived aerial shoot with numerous whorls of branches, with a large, sessile, apiculate, green terminal cone and with numerous small cones on the branches. The ring or calyx at the base of the cone bears sporangia on the upper side. The plant is said to attain a length of 20 ft. or more. In *E. myriochaetum* there is a considerable reduction in size but there are still abundant whorls of branches. *E. ramosissimum* is still more reduced and the branch whorls are rather sporadic. In *E. laevigatum* the branches are very sporadic and often entirely absent. The next species on the list, *E. fluviatile*, belongs to a different line and connects more closely with *E. giganteum* but is in most respects on a much higher level than *E. laevigatum*. *E. fluviatile*

has whorls of branches and bands of stomata like *E. giganteum*. It has advanced very decidedly from the primitive condition represented by *E. giganteum*. The aerial stem is annual instead of perennial, the cone is without a point because of a more prompt determination of the floral axis, the calyx is usually entirely sterile, and there is a rather definite beginning of the evolution of a peduncle. The fertile and sterile shoots show no dimorphism except that the one has a cone and the other has none. In *E. silvaticum*, aside from its specific specializations, there are several important advances. The fertile and sterile shoots are decidedly dimorphic. The fertile shoot has little chlorophyll at first and no whorls of branches and the peduncle is quite prominent. Later whorls of green branches develop on the fertile stem and only the cone and its peduncle wither after the spores are shed. The cones are differentiated underground at an early stage and not delayed until after the aerial stems have developed as in the preceding species. In *E. arvense* the progression is carried to the extreme. The fertile and sterile shoots are decidedly dimorphic. The fertile shoot develops no branches and has little or no chlorophyll. The differentiation of the flower is begun underground at the inception of the shoot during the previous season. The entire fertile stem withers in a few days after it comes out of the ground when the spores are shed. The peduncle is very highly developed and the whorl branches are solid and have but three or four ridges on the internodes.

It is a remarkable fact that in so far as the morphology has been worked out the evolution of the gametophyte moves forward consistently in the same general direction. The gametophytes are comparatively large in *E. laevigatum* and *E. debile* and are hermaphroditic while in *E. arvense* they are comparatively small and are normally unisexual. In the hermaphroditic species the archegonia are devloped first and later the antheridia. There are sometimes as many as 200 archegonia on a single hermaphroditic plant. The embryology also indicates that the first four species of the given series are the more primitive and nearer the eusporangiate ferns than the last three.

Comparing the sporophytes of the last species with the first, we note the following additions to the hereditary potentialities which represent the progressive evolutionary movements that

have taken place to bring *E. arvense* to its high level of complexity:

1. The aerial shoot evolves from the perennial to the annual condition. This same movement appears in two other lines of Equisetum and has taken place in large numbers of the higher groups of plants.
2. The fertile shoot changes from an abundantly branched condition to a specialized stem without branches.
3. The fertile shoot including the flower, has lost nearly all of its chlorophyll and is brown in color. This loss of chlorophyll is a general evolutionary movement in all the higher flowers.
4. The fertile shoot evolves from a long-lived system to a very short-lived system, withering soon after emerging from the ground.
5. The fertile shoot is developed entirely underground, complete for spore dispersal and differentiated from the beginning.
6. The cones are more definitely determinate and do not have a vegetative point. This progression toward greater promptness in determination of the reproductive axis is a universal trend in all the higher plants.
7. There is a distinct reduction in the number of sporophylls because of the earlier determination and this movement is also practically universal in floral evolution.
8. The calyx evolves from a sporangium-bearing whorl to a completely sterile structure, thus giving a definite, sterile perianth, the first to appear among the living species of vascular plants.
9. A prominent peduncle has evolved below the flower, duplicating the corresponding evolutionary movement in *Lycopodium*. The peduncle is very generally evolved in the plants above this level.
10. The fluctuation between flower and vegetative tip with the development of intermediate semi-sterile cones is quite rare while in the species on a lower level it is exceedingly common. In the higher flowering plants intermediate shoots are exceedingly rare, in fact practically non-existent.
11. The fluctuation in the length of the vegetative internodes is less common than in the lower species.
12. The aerial shoots are very much smaller and this movement is prominent in every section of the genus.
13. Proliferation, which represents a return of the reproductive axis to the most primitive condition is much less common than in species on a lower level belonging to the same general group, like *E. fluviatile* for example. The same condition holds for low types of flowers in higher subkingdoms. Proliferation is common in such genera as *Araucaria*, *Larix*, and *Rosa*, while it is absent or exceedingly rare in the highest.
14. The number of teeth and sheath segments of the branches is very definite in *E. arvense*, being three or four, while in the lower species the numbers fluctuate decidedly.
15. Cones are rarely developed on branches, even in related species where branch whorls are still present on the fertile shoots, while in *E. giganteum* and other low species branch cones are a regular feature.

THE GENUS SMILAX.

Smilax represents one of the very extremely specialized groups of the monocotyls. The greenbrier family is plainly closely related to the Convallariatæ as represented by *Polygonatum*. In fact, Smilax is apparently only a specialized branch of the same phylogenetic series. The main series of progression is well represented by the following species:

1, *Polygonatum commutatum;* 2, *Smilax ecirrhata;* 3, *S. herbacea;* 4, *S. pumila;* 5, *S. glauca;* 6, *S. hispida;* 7, *S. lanceolata.*

Polygonatum commutatum has a creeping, more or less fleshy rhizome with an annual aerial herbaceous shoot usually from 3–6 feet high with about 20 leaves, the internodes being about 1–1½ in. long except the basal one which is often 16 in. or more in length. It has bisporangiate flowers and the anthers have four microsporangia. There are no tendrils. In most other general characters it is much like an herbaceous *Smilax*. Both in *Polygonatum* and *Smilax* there are two-ranked leaves which condition is a very general culmination in the monocotyls in the evolution from a three-spiral condition. In the lowest species of *Smilax*, namely, *S. ecirrhata*, the two-ranked condition is not very definite.

Now in passing from *Polygonatum commutatum* to *Smilax ecirrhata* four very important progressive changes are in evidence. The plants become diecious, the microsporangia are reduced to two in the anther, there is a slight development of woodiness in the lower part of the plant, brought about by the hardening of the pith, and a potentiality is added for developing tendrils on the petioles. The new tendril heredity is only active toward the end of the ontogeny of the aerial shoot. The tendril potentiality has been added to the previous normal leaf heredity. The old potentiality is not destroyed, but is active in the juvenile condition. The new tendril heredity is latent until the juvenile physiological gradient is passed, when the functional conditions of maturity throw it into play. In this case, therefore, there is recapitulation of the ancestral character at the beginning of the ontogeny. Very frequently the new heredity added to a system is such that it becomes active in the juvenile condition and recapitulation may then occur at the end of the ontogeny or even in the middle stage. In *S. ecirrhata*, if the plants are small, so that growth does not

continue long enough, there will be no tendrils whatever even on the last leaves.

Passing over to *Smilax herbacea*, we have the same general type of plant although the tendrils usually appear somewhat earlier. The first tendrils usually appear on the 5th to 10th leaf. All the subsequent leaves will have tendrils normally. A new factor is now introduced which is destined when fully evolved to produce a most remarkable monocotyl. This is a potentiality for rapid and prolonged growth. This new potentiality causes the mature plant to elongate rapidly and thus a viny stem is developed which, because of the presence of tendrils on the leaves gives the plant a slight climbing ability. It will be noted that the tendrils were evolved in a plant which has no climbing ability otherwise. *S. herbacea* is somewhat less woody than *S. ecirrhata*.

In *Smilax pumila* the rambling factor is considerably augmented and the stem which is still terete is weak or reclining and still only about 2–6 ft. long. The woodiness of the stem is not very marked, but is nevertheless much more prominent than in the preceding species. As intimated above, the woodiness in all the species of *Smilax* is a new characteristic and is produced by the hardening of the walls of the ground tissue or pith and not by an increase of xylem in the vascular bundles. It is entirely a secondary evolutionary acquisition laid down on top of the original potentiality responsible for ordinary pith parenchyma. The petioles and tendrils of *S. pumila* are also not very woody. All of the four species considered so far have prominently elongated basal internodes, usually the first two above ground. The lowest internode is usually from 4–12 in. long and the second from 3–6 in. The internodes between the foliage leaves usually range as follows: *Polygonatum commutatum*, 1–1½ in.; *Smilax ecirrhata*, 1–2 in.; *S. herbacea*, 1–3 in.; *S. pumila*, 1–4 in.

In passing up to number 5, *Smilax glauca*, we meet the first typical greenbrier. The stem is completely woody and the woodiness extends to the petiole base and tendrils. The leaf blade is deciduous beyond this woody base. The internodes are perceptibly longer on the main axis than in the preceding species, usually being from 2½–4 in. long. The rhizome is long and slender and prickly but somewhat tuberous. The tendrils appear earlier in the ontogeny, usually on the fourth to sixth leaf. The stem has prickles which is a new evolution and

these are present on most woody species. The stems are usually about 6 to 12 ft. long and definitely climbing, but still inclined to be somewhat bushy. The rambling habit is far from being completely evolved. The ultimate twigs are definitely quadrangular. Many of the woody species have these quadrangular twigs not because of any advantage or disadvantage, for similar quadrangular twigs appear in many monocotyls and dicotyls, in herbs as well as woody plants, in aquatics as well as in ordinary aerial mesophytes. The quadrangular character is frequently associated with the attainment of the two-ranked condition or opposite leaves. It represents an evolutionary progression from a radially symmetrical system to a bilateral system. Ornamental white spots are usually in evidence on the leaves of *S. glauca*. There is also a progressive reduction of the ovulary in the series. *Polygonatum* has several ovules (6–2) in each cavity; in the herbaceous species of *Smilax* there are two ovules in each cavity; while in the higher group, or woody species, there is but one ovule in each cavity. Thus the ovulary is approaching the ultimate unilocular condition.

The next evolutionary step gives a typical greenbrier in *Smilax hispida*. The rapid growth factor is greatly increased so that this liana frequently climbs up in trees 30 to 45 ft.; the internodes of the main stem are commonly 4–10 in. long. The stems are usually also very prickly. In general the progression toward an ideal liana is far advanced.

Taking *Smilax lanceolata*, or Florida Smilax, as an ideally developed liana species, several prominent orthogenetic advances are in evidence. The plant grows at an enormously rapid rate and the internodes are frequently over 1 ft. long. The plant often climbs up 70 to 80 ft. to the top of tall trees, and has scattered prickles on the main stem, although none on the branchlets. Only the first or second leaves are usually without tendrils. The tendrils appear in successively earlier stages of the ontogeny as one passes through the *Smilax* series. The leaves are usually decidedly narrowed and have only 3–5 nerves (mostly 3) instead of the 15–21 nerves present in *Polygonatum* or the 5–13 nerves present in the species from Nos. 2–6. The leaves have become persistent, which might, of course, be a condition handed down from the ancestral type in the series. In the closely related *S. laurifolia*, the fruit ripens only the second year. The underground system consists of large tuberous stems suggesting very large potatoes. These

tubers also represent the extreme when compared with the preceding species, beginning with the creeping rhizomes of *Polygonatum*.

When one considers carefully the changes which take place step by step in this series of seven species, he discovers a most remarkable building up process which shows how evolution progresses by the addition of new character potentialities on top of the old and by the orthogenetic perfection of the characters when they are once added. All of these plants are dwellers in the forest and thicket. The series is not to be explained on any assumption of impelling environments nor by any notions of special utility, although a Lamarckian might here actually find a special utility in the base of the petiole and the tendrils. But as is evident from the analysis given above, the tendrils and woodiness began to appear before there was any use for them and the beginning of the stretch habit appeared before there was any real climbing to be done. As to the leaf forming the abscission at the outer end of the petiole instead of at the base, which might seem like a plain case of survival through advantage to a believer in Darwinism, the same thing occurs in species of *Rubus* and other plants where no tendrils are present and where no stem is to be held up to a support. The teleological explanation of quadrangular twigs, prickly stems, fruit delaying its maturity to the second year, and especially the prickles on the underground rhizomes should certainly strain the credulity of even the most credulous to the breaking point.

THE GENUS VIOLA.

The violets show a very beautiful orthogenetic movement from the bottom to the top of the series. The following species will represent the main progression:

1, *Crocanthemum canadense;* 2, *Cubelium concolor;* 3, *Viola canadensis;* 4, *V. odorata;* 5, *V. pallens;* 6, *V. papilionacea;* 7, *V. palmata;* 8, *V. pedatifida.*

The ancestral type of the violet family may in a general way be represented by *Crocanthemum canadense* which has erect stems, sometimes 2 ft. high, short-petioled leaves, only slightly zygomorphic flowers, and numerous stamens. It has both showy petaliferous flowers and apetalous cleistogamous ones. The cleistogamous flowers are, of course, a specialization which might not be present in the lower violets.

In *Cubelium concolor* the more typical violet characters are already evolved. Although the stem is still erect with short-petioled leaves and short-peduncled flowers, the flowers are decidedly zygomorphic and the stamens are reduced to five.

In *Viola canadensis* the generic characters of *Viola* have been fully attained and the sepals are highly specialized, being more or less prolonged posteriorly. This character is still missing in *Cubelium*. The two lower stamens are also specialized, being distinctly spurred. The flowers are thus much more zygomorphic both externally and internally. Two other very characteristic violet characters are evolved to a moderate degree. Although the plant still has an erect aerial stem, the petioles and peduncles show a distinct tendency to elongate. This movement will end in a very extreme condition in the higher geophilous violets. It is to be noted again that the evolutionary movement begins before there is any need of it and before the plants show any definite tendency toward geophily. In this species petaliferous flowers are still often produced throughout the summer.

The group of violets to which *Viola odorata* belongs shows a strong movement toward the development of the geophilous condition in that there are long and slender leafy stolons produced above ground. The most remarkable potentiality added is the dimorphic production of flowers. This plant as well as most of the species on a higher level in the same phyletic series has both the ordinary showy flowers and apetalous cleistogamous flowers which have only two functional stamens.

In *Viola pallens* the orthogenetic movement has advanced further and the plant has long slender rhizomes and in addition slender creeping stolons.

Viola papilionacea represents a typical blue violet. The stem has become a thick, fleshy rhizome without aerial runners; the petioles and peduncles of the showy flowers are exceedingly long while the peduncles of the cleistogamous flowers are rather short; the showy flowers are decidedly zygomorphic, with three distinct types of petals.

In *Viola palmata* the rhizome is more extreme and the leaves are palmately 5–11-lobed, while in *V. pedatifida* the extreme of the series is reached in a plant with short erect rhizomes and palmately multifid leaves with very narrow segments.

The evolution of cleistogamous flowers in a series which has only showy insect pollinated flowers at the lower levels shows how incorrect the older hypotheses of evolution, like use and disuse and natural selection, were; for these higher violets all produce showy flowers which are extensively visited by insects but which produce little or no seed. During the summer period the cleistogamous flowers are developed in great abundance and on the same individuals and produce large quantities of seed from which the species is abundantly propagated. This development of cleistogamous and sometimes parthenogenetic flowers at the ends of many evolutionary series of Anthophyta of both entomophilous and anemophilous plants plainly indicates that the libraries of books and articles written to prove that the showiness of the flower was evolved to attract insects to insure cross pollination are to be considered largely in the same light as our mother goose fairy-stories. Nectar glands and fragrant odors are associated with some sporophylls of ferns long before there were any flowers and before there was any pollen to be carried, and attractiveness of beautiful colors and even zygomorphy are frequently in evidence in the lower wind pollinated series, while many of the entomophilous series end in exceedingly inconspicuous types.

A CONIFER SERIES.

There are many exceedingly interesting progressive series in the Coniferæ. The following one will illustrate a progressive building up of a very complex hereditary system from a comparatively simple one, the series running through two families and a number of genera.

1, *Araucaria imbricata;* 2, *Cunninghamia sinensis;* 3, *Sequoia sempervirens;* 4, *Pseudotsuga mucronata;* 5, *Picea abies;* 6, *Cedrus lebani;* 7, *Pinus strobus;* 8, *Pinus serotina;* 9, *Pinus radiata;* 10, *Pinus muricata.*

Araucaria imbricata is a very primitive type of conifer. It has a rhythmical development of branches on the main stem and the foliage leaves are close-set in spirals. The leaves of the main stem have no developed buds in their axils except at certain intervals and are all of the same general type. There are no bud-scale leaves, the resting period being simply marked off by a zone of shorter, smaller green leaves. The leaves have no phototropic ability. The whorl branches also have

sporadic development of buds in the leaf axils and these develop into prominent secondary branches which are a sort of dwarf branch. There are no internodes on the plant. The staminate and carpellate cones terminate leafy branches and the sporophylls are very leaf-like.

In passing up to *Cunninghamia sinensis* there is evident a considerable narrowing of the leaves and the leaves also show a phototropic reaction. There is a slight beginning of a resting bud with specialized bud scales. The staminate cones are in clusters and the carpellate cones also show a tendency to be clustered although they are often solitary at the end of a leafy shoot. There is a considerable difference between sporophylls, and foliage leaves. The carpels, however, still show a distinct midrib and other leaf characters.

Sequoia sempervirens shows an increase in the evolution of the resting bud and bud scales. The leaves are linear and react definitely to light and the carpels are highly specialized and thickened. These three species form a suitable, primitive background for the pine series proper.

In *Pseudotsuga mucronata* the winter bud is well evolved and shows dry scale leaves. The carpels have large carpellate bracts and the thickening takes place in a different manner from that in *Sequoia*, the lower part of the carpel back of the seeds being developed into a distinct structure, the ovuliferous scale. The tree, therefore, has four distinct kinds of leaves, instead of three as in *Araucaria imbricata*. The foliage leaves are linear, being evolved to the same condition as in *Sequoia sempervirens*. *Pseudotsuga* along with the remaining genera of Pinaceæ has winged pollen in contrast to the lower Taxodiaceæ and Araucariales.

In *Picea abies* the leaves have become prismatic but still show a slight reaction to light in bending away from under the twig. The carpellate bracts have been reduced and are hidden beneath the ovuliferous scales which are much as in *Pseudotsuga mucronata*. There are sporadic buds which develop into small branches in numerous leaf axils between the main branch whorls and the branches also show sporadic bud and branch development in some leaf axils. The plant is thus definitely evolving to a less simple, less symmetrical system.

Cedrus lebani shows a considerable evolutionary advance in the acquisition of sporadic dwarf branches which, however, have indefinite growth. The foliage leaves on the dwarf branches are

beginning to elongate and are in the first stages of the evolution of needle leaves. The scale leaves of the dwarf branches are somewhat different from those of the long branches. The leaves of the long branches are also different from the foliage leaves of the dwarf branches. The ovuliferous scales, although of the same general type as in *Pseudotsuga* and *Picea*, are more thickened and woody. The cedar thus has two kinds of foliage leaves, two kinds of bud scale leaves and two kinds of sporophylls.

Now, passing over to the genus Pinus, several important new characters are again added. In *Pinus strobus* the ovuliferous scale shows three new characteristics which are not present in *Pseudotsuga*. The scale is elongated, is showing considerable woodiness and has a peculiar ornamental tip. The leaves on the main axis and long branches are changed to dry scales and each one develops a bud which gives rise to a dwarf branch. These dwarf branches are determinate in growth and after developing bud scale leaves and five foliage leaves are completely arrested in further development. Thus vegetative determinateness is again evolved. After several years each dwarf branch is self-pruned by the development of an abscission layer. The foliage leaves are longer and more definitely needles than in the cedars and larches. The white pine, therefore, has developed an enormous efficiency for producing axillary buds when compared with *Araucaria* or *Cunninghamia*. In the next higher family beyond the pines, the Juniperaceæ, as for example *Juniperus barbadensis*, the number of buds and twigs in a comparable branch system is again enormously increased when compared with *Pinus* although bud development is sporadic and many leaf axils do not produce functional buds. *Pinus* has four kinds of mature vegetative leaves besides the two kinds of sporophylls or twice as many general types as *Araucaria imbricata*. In addition there is still a seventh kind of leaves present in the system, the special juvenile leaves of the seedling to say nothing of a distinct kind of cotyledons. The basal elongation of the needle leaves becomes very pronounced in some species of pines. In the white pine there is a peduncle on the subterminal carpellate cones, but this is a specialization which is not continued in the yellow pine group, represented by the last three species of the series given, although these have a very marked modification of the lower carpels. The cones ripen promptly in the summer of

the second season. The pollen, of course, has the highly specialized two wings or sack-like appendages.

Pinus serotina shows a decided specialization in developing "wrapper" scale leaves on the dwarf branches. The foliage leaves are reduced to three on the dwarf branch and are more extremely evolved as elongated, rigid needle-leaves. The ovuliferous scales are more elongated, much more woody, and have a much more extreme, ornamental apex than in *Pinus strobus*. The cones are lateral showing the beginning of irregular branch development as in *Picea*. There is also a very decided shortening of the base of the carpellate floral axis, giving rise to a wide sterile zone of carpels. This is again a first step in the evolution of a perianth. The terminal carpels also show a different development. Thus there are three general types of carpels and three rather distinct regions of the cone to be definitely recognized. These differences are less pronounced in the lower members of the series.

In *Pinus radiata* a striking new property is added, resulting in a decided zygomorphy of the carpellate cone. Zygomorphy is a characteristic of nearly all the highest types of flowers of the Anthophyta. The ovuliferous scales are much larger on the outer side than on the inner and the tips have prominent rounded protuberances. Thus there are really four general types of carpels which, of course, intergrade with each other. With the five kinds of vegetative leaves and counting but one type of stamens, this pine has ten kinds of leaves besides the cotyledons. This certainly indicates a decided evolutionary advance in complexity when compared with the three types present in *Araucaria imbricata*, the two types in some of the higher ferns, or the single type present in many of the lower ferns, where no morphological difference is to be observed between sporophyll and foliage leaf except the presence of sporangia on the former.

Pinus muricata has much the same general characteristics as *P. radiata* but the ovuliferous scales are more elaborated. The knob below the apex is flattened and armed with a stiff flattened spine. The cones are decidedly zygomorphic as in *P. radiata*. There are but two leaves on the dwarf branches, which is the usual limit to determinateness in the higher pines except in one species of nut pine in which there is mostly but a single leaf on a dwarf branch. The higher pines are commonly characterized by irregular development of their crowns. This

is especially due to the intercalary development of long branches between the rhythmical branch whorls. In some species, as for example *Pinus contorta*, the old crowns are sometimes grotesquely irregular in contrast to the regular rhythmical symmetry of the lower white pines or the remarkable, repetitive symmetry of an araucarian.

In a tree fern there is normally but one terminal bud which gives a single type of morphological reaction; in *Araucaria imbricata* there are four kinds of stem bud reactions, the terminal bud, the primary and secondary branch buds, the carpellate cone bud, and the staminate cone bud. There is very little difference in the reaction of the main stem bud and the branch buds, but the former differentiates a radially symmetrical branch system while the latter differentiates a more or less dorsivential sytem which becomes extremely fixed so that when grown as a cutting it gives rise to an unsymmetrical tree. In *Pseudotsuga* there is the same general difference of four types of bud reaction, but the difference between the terminal stem bud reaction and the lateral twig is very much greater. In *Pinus* there are in general five types of stem bud reactions, the terminal stem bud, the main and lateral branch buds, the dwarf branch buds, the carpellate cone bud, and the staminate cone bud. Thus the genus *Pinus* again shows an extremely complex reaction system in its buds and plainly stands at the end of its phyletic series in this respect also.

It is truly astonishing that in this conifer series not only the general external organography and morphology show this orthogenetic accumulation of a more and more complex hereditary system but that there are several lines of minute characteristics which went through a closely parallel movement at the same time and in the same direction. Thus the lower gymnosperms, like *Cycas* and *Ginkgo*, have two cotyledons and the same number is present in *Araucaria*, in *Cunninghamia*, and in *Sequoia sempervirens*, while in *Sequoia washingtoniana* there are three to six and in the various species of *Pinus* the number range from five to fifteen. Thus the complexity of cotyledon development has kept step with the evolution of the general complexity of the pines. In the lower Ptenophyta which presumably represent the mother phylum of the Strobilophyta there is a single embryonic leaf. The parallel series or order of Taxales also evolved polycotyledony but not to so extreme a condition as the Pinales. This development of many coty-

ledons is a derived condition involving the determination of correlation centers in the ring of tissue surrounding the terminal bud of the embryo. There is much variation in the definiteness of the interaction and often two centers of activity do not become developed sufficiently for independent action, thus giving rise to twin cotyledons or in some cases apparently enlarged simple cotyledons with double vascular strands. Such phenomena are, of course, common in other similar structures, as the very common development of double or broad sporophylls in *Equisetum*. The development of double cotyledons and cotyledonary tubes has given rise to controversies and the development of a contrary hypothesis that the polycotyledonary condition was the original and the dicotyledonary one the derived condition. But this would go counter to all the complex progressive movements and is not to be taken seriously. There is no basis for turning evolution topsy-turvy because of a fantastic method of interpretation of abnormalities.

In Cycas and *Ginkgo* a single embryo is organized from the egg, which is the usual condition from the liverworts on up. In *Araucaria* there is also a simple embryo without a rosette at the basal end beyond the suspensor. Passing up to the Pinaceæ one finds a decided and progressive advancement toward the most extreme condition. In *Pseudotsuga* a single embryo develops from the egg and a long suspensor but apparently no rosette cells. In *Picea* and *Abies* a single embryo is developed with rosette cells beyond the base of the long suspensor cells and essentially the same condition exists in *Larix* which in general morphology represents a more advanced condition. But in *Tsuga* a new condition is introduced and the condition of cleavage polyembryony is established, four embryos developing from a single egg. *Cedrus* which in some respects is on a lower stage of evolution than *Larix* has advanced its embryogeny to the extreme condition approaching that of the pine. There is not only cleavage polyembryony but rosette embryos are also produced. The culmination of the embryonic complexity of the Pinaceæ is reached in the genus *Pinus* where the egg, through cleavage polyembryony, develops four incipient embryos at the outer end of the long suspensor and four prominent rosette embryos at the basal end. In Biota cleavage polyembryony is even much more extreme than in the pines. Thus it is seen that the embryonic evolution moves in complete

harmony in the same direction and in general keeps pace with a large number of progressive characters, thus giving rise to the exceedingly complex reaction systems present in the highest pines.

The advancement in simple bilaterality of the sporophylls is also plainly in evidence in this series. In *Araucaria* there is one central seed, in *Cunninghamia* three, in *Sequoia* four to nine, while in some of the more specialized genera of Taxodiaceæ and in the Pinaceæ the number is uniformly two, evenly balanced on the two sides of the carpel.

Another interesting development is shown by the time of maturing of the carpellate cones. Primitive forms apparently all matured their cones in a single season as is the case in *Cycas*, *Pseudotsuga*, *Picea* and *Tsuga*. In *Larix* the fruiting cones also mature the first year while in *Pinus*, the culmination of the series, the cones do not ripen until the second year. In *Juniperus*, belonging to a higher related series, some species mature their cones the first year and some the second.

The progressive reduction of the male gametophyte in the conifers also parallels the other general movements. In *Araucaria*, the pollengrain shows its primitive character by developing from 20 to 44 vegetative thallus cells (prothallial cells) besides the spermatogenous, stalk, and tube cells. In *Pinus*, which stands at the top of the Pinaceæ and far above the Araucariaceæ in nearly all characteristics, two minute and evanescent vegetative thallus cells and finally spermatogenous, stalk, and tube are produced. In the Juniperaceæ, the extreme group of the Pinales, no vegetative thallus cells whatever are developed and the pollengrain usually contains only two cells. The Taxales show a higher level in male gametophyte reduction at the base than the Araucariales, as would be expected. In some species of *Podocarpus* as many as 8 vegetative thallus cells may be developed in the pollengrain, and in various other species and related genera there is a reduction, until the highest condition is attained in the Taxaceæ, where no vegetative thallus cells are produced, just as in the Juniperaceæ, but the first division gives rise directly to the spermatogenous and tube nuclei. These plants are in this respect on the same level of advancement as most of the Angiospermæ. It is remarkable that just as in the Pinales, the extreme reduction of the male gametophyte is in the Taxales also correlated with other extreme evolutionary morphological developments. The

reduction of the male gametophyte is thus consistently orthogenetic in a most remarkable manner.

A study of the wood in the series also shows a remarkably consistent progression. The cycads have a multiseriate condition of the bordered pits on the tracheids and the pits are somewhat elongated. This is evidently the primitive condition for living gymnosperms. In *Araucaria* there are also two or more rows of bordered pits usually present on the radial walls of the tracheids while in *Cunninghamia* there is mostly a single row. This specialization is carried through to the highest pines and the bordered pits become very circular instead of showing the elongated condition common in *Cycas*.

In *Pseudotsuga* the wood contains a number of characteristics which indicate a lower condition than that shown in *Pinus*. In *Pinus strobus* the upper and lower walls of the few and small ray tracheids are smooth and have the radial walls of each ray parenchyma cell communicating by one or two large simple pits with each adjacent wood tracheid. In the yellow pines generally, like *Pinus muricata* or *P. virginiana*, a much more complex reaction system is in evidence. The upper and lower walls of the small and numerous ray tracheids are sculptured with ornamental reticulations and the radial walls of each ray parenchyma cell has three to six rather small simple pits communicating with each adjacent wood tracheid. Thus the evolution of the wood elements is moving in harmony with numerous other orthogenetic progressions.

Finally another most remarkable parallel movement took place in relation to resin cells and resin passages. This series was worked out by Penhallow. Resin cells occur in the more primitive conifers and are scattered in the bast; in the next stage they occur in zones and finally they are definitely segregated. Segregated resin cells may give rise to resin cysts, as are present in *Sequoia*, *Tsuga*, and *Abies*. In *Pseudotsuga*, *Picea*, and *Larix*, the continuous system of resin canals are present and show their derivation from resin cysts by the constricted walls. In *Pinus* the walls are no longer constricted and are lined by a thin-walled epithelium, except in a few types where thick-walled cells are interspersed with the thin-walled ones. This series coincides very closely with the other numerous orthogenetic movements. Only *Pseudotsuga* seems to have marched ahead a little of its expected position in this respect. The series indicates again that the Pinaceæ are a

highly evolved type of conifers and that *Pinus* is the most specialized genus of the family.

In some genera of the Pinaceæ resin canals are absent from the woody tissues of the stem except in the first annual ring of vigorously growing shoots, as in *Abies*, or the resin canals may occur only traumatically. In these cases one may assume that in such a condition a new potentiality has been added which under normal conditions interferes with the expression of the character or, on the other hand, the potentiality for resin canals may have been added even after the primary phylum had been segregated into the secondary phyla as *Abies*, *Tsuga*, *Cedrus*, etc., and then never was able normally to come to expression because the inhibiting factor had been acquired previously.

When one considers all these remarkable orthogenetic movements running from *Araucaria* to *Pinus* in the same general direction, one begins to get some superficial notion of the wonderful process which was responsible for the taxonomic system as we find it in the world today. What was it that kept all of these movements marching step by step, with hardly a deviation, in a definite direction to the end? What kept the mutative processes of the hereditary potentialities in the straight and narrow path during the long course from the comparatively simple araucarians to the highly complex reaction systems of the higher yellow pines? The very thought of special utility suggests a childish question, the notion of teleological selection is quite preposterous, the idea of a direct response to environment is ridiculous. Such notions have no correspondence with the actuality. So we will finally have to get down to the study of the nature and structure of protoplasm, yes, even to a study of the dust of the earth from which it had its origin, if we are ever to even approach the immediate causes involved in the evolutionary process.

Now this inventory of the cumulative evolution of hereditary potentialities giving rise at each stage to more and more complex characters and reactions by the addition of new heredity to the old cannot be properly appreciated unless one actually studies the complete series containing the additions step by step. If this is done then one must obtain a firm conviction that the order of presentation given above is the true evolutionary order and represents the actual general trend of the evolving system. Such a study properly undertaken will

plainly show that evolution is cumulative and progressive, "precept upon precept, line upon line," potentiality upon potentiality. There is, in general, nothing hap-hazard about it. It pays no special attention to conditions and environments except in so far as the environment may or may not permit survival. In the series given all the numerous changes and additions have an equal survival value in many diverse habitats. The matter of survival is not involved at all in the characters discussed. Plants with practically none of the peculiarities are to be found prospering side by side with those that have the peculiarities. Take for example the evolution of winged pollen mentioned above. This has appeared independently in entirely different conifer lines, and conifer species with winged pollen and without thrive in the same forest. All the members of the evolved series were surrounded by the same air and subject to the same winds. The wings are not at all necessary for survival. On the other hand, they do no harm. Pollination is assured whether wings are present or not.

The whole evolutionary process, described in the five examples, presents the working out of a wonderful cosmos, a system unfolding according to some fundamental principle which we have not discovered scientifically but which is nevertheless clearly and inevitably at work in bringing out the remarkable succession of potentialities in a substance, the protoplasm, which must at the beginning have been an undifferentiated system with enormous possibilities.

The present studies show that evolution has forced its way through the circumstances of environment, ever leading forward, and that new complexities and new efficiencies have been added from time to time through an evolutionary creative principle in the same way that the creative human mind adds improvements, complexities and efficiencies to its machines and mechanical devices year by year and from age to age, until the perfect and the ideal are attained at the end, whether it be an automobile, a flying machine, a compound microscope, or a radio receiving instrument. And thus it is that when we compare a dandelion with a man we find that, because of a common forward progressive and accumulative movement they are as much alike in important potentialities which they have evolved in common as they are both profoundly different from one of the primitive members of the living kingdom, for example, a nonsexual, holophytic, unicellular bacterium.

DRAINAGE CHANGES IN THE VICINITY OF LOUDONVILLE, OHIO.

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INTRODUCTION.

In a previous number of the Ohio Journal of Science[1] the writer gave reasons for believing that the preglacial drainage from Wooster was southward toward Shreve instead of eastward toward Orrville, as postulated by Todd.[2] Obviously, if the waters could not escape by a route to the eastward they must have flowed either to the south toward the Walhonding or northward toward Lake Erie. In this paper an attempt is made to find an exit for the extensive drainage system called by Dr. Todd, the Old Mohican.

The writer takes this opportunity to give credit to other workers in this area, Leverett, Hubbard, Conrey and Coffey, all of whom have made contributions to the drainage and glacial problems.

PREGLACIAL DRAINAGE.

In preglacial time a major divide extended in a northwesterly direction through Ohio, from a point in western Belmont County, through northeastern Guernsey, Tuscarawas and Holmes counties and extreme southern Ashland and Richland counties. This divide separated the drainage leading northward toward the Lake Erie basin and the drainage to the south which led westward past Buckeye Lake. The area discussed in this paper lies to the north of the above mentioned divide.

Examination of the Loudonville quadrangle reveals the existence of a broad valley which extends from Loudonville to Wooster. This valley, now followed by the Pittsburgh and Fort Wayne Division of the Pennsylvania Railroad, was

[1]Ver Steeg, Karl. Drainage Changes in the Vicinity of Wooster, Ohio. Ohio Journal of Science, Vol. 30, No. 5, September, 1930.

[2]Todd, J. H. Some Observations on the Preglacial Drainage of Wayne and Adjacent Counties. Ohio State Academy of Science, Special Papers, No. 3, pp. 46–67, December, 1900.

occupied by a large stream in preglacial time. Todd, who called it the Old Mohican, traced it from Mansfield to Loudonville and Shreve, where its course he believed was northeastward to Wooster, from which point he assumed it extended across a broad divide to Orrville, where it presumably followed the old valley now occupied by Little Chippewa Creek, taking a northwesterly course, leaving Wayne County north of Sterling. From this location he believed its channel led northward by way of Chippewa Lake and into the valley of the West Branch of the Rocky River. The objection to this route appears to be that there is no evidence of the existence, in preglacial time, of a channel across the divide between Wooster and Orrville.[3] Therefore it is necessary to find another course by a different route. It has been suggested that the stream may have flowed south by way of the Killbuck valley into the Walhonding. But there are good reasons why this could not have been its course. The evidence appears quite convincing that the major divide, mentioned above, crosses the present course of Killbuck Creek near the town of Killbuck. This watershed was high, 1,300–1,400 feet above sea level in many places, separating the streams in the basin now occupied by the Tuscarawas and Walhonding rivers and which had its outlet to the west, from the streams which flowed northward to the Erie basin. The divide continues westward to a point south of Nashville and from there to a position west of Spellacy, extending between the tributaries of the Clear Fork, flowing northward and those flowing south into the Kokosing River. In preglacial time this divide separated a stream, now the lower Killbuck, flowing southward and another flowing northward into the large stream which occupied the valley from Wooster to Shreve. There is further evidence which seems to favor the above conclusion; the Killbuck valley narrows markedly in the direction in which the stream flows and is narrowest at the col near the village of Killbuck, where the water was forced over the divide as a result of damming by glacial action to the north. The tributaries which flow into this portion of the Killbuck, from Kauke to the col, flow into the trunk stream at an angle normal for a stream flowing north. South of the col, the tributaries of the Killbuck are normal for a stream which flowed southward in preglacial time. This part of the Killbuck widens gradually to

[3]Ibid. 1, pp. 309–314.

the south, being widest where it enters the Walhonding River. It appears conclusive to the writer that the Old Mohican did not flow southward by way of the valley of the Killbuck. The drainage must necessarily have been northward from the major divide toward the Lake Erie basin. The waters could

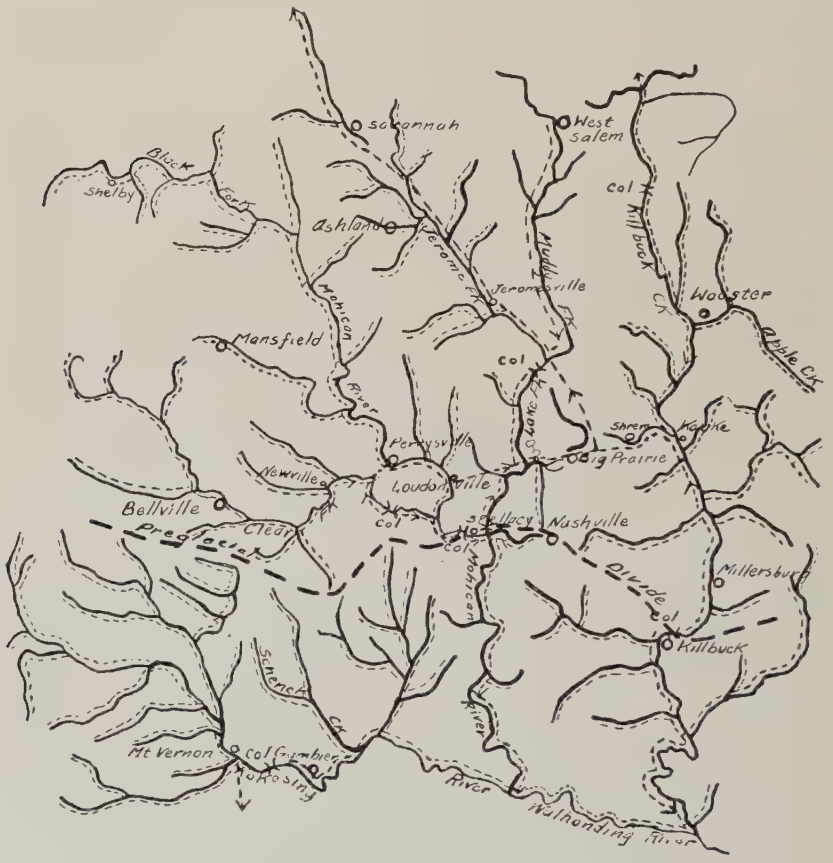

FIG. 1. Sketch showing drainage changes; dotted lines indicate the preglacial drainage.

not escape across the divide between Wooster and Orrville, nor through the upper Killbuck valley occupied by the Baltimore and Ohio Railroad; in the first instance bed rock completely shuts off the exit and in the latter case the Killbuck valley widens southward from a point between Armstrong and Overton, where a preglacial col existed, indicating that this valley was occupied by a tributary which flowed south-

ward. The only outlet for the waters was by way of the broad valley which extends northward from Big Prairie and Custaloga. The most logical route northward is the valley of the Jerome Fork. It does not narrow to the north as the one to the east occupied by Muddy Fork which is much narrower than the Jerome Fork valley. It is evident that Muddy Fork valley in preglacial time was the site of a stream which flowed south. The greatest objection to the northward route by way

FIG. 2. Map showing the direction of the preglacial drainage, the position of the cols and the location of the Mohican Park.

of Jerome Fork valley seems to be the angle at which it meets Muddy Fork. It is such as to indicate that the two streams joined west of Blachleysville and flowed south into the Old Mohican at Custaloga. But the fact that the Muddy Fork valley has a trend contrary to what one would expect if the main stream flowed north in Jerome Fork valley is not fatal to the argument. The trunk stream appears to have flowed northwestward past Jeromesville and Savannah and from there by way of the Vermilion River valley. Because the exit of the waters is shut off everywhere except by this route, seems to the writer to be the best argument for such a course.

Southwest of Perrysville there appears to be a broad preglacial valley about a mile long, filled with glacial drift. Doubtless this was the preglacial course of the Clear Fork of the Old Mohican. In T. 19 N. and R. 16 W., sections 8 and 17 in Mohican Park there existed a divide, which separated a tributary to the Clear Fork from another flowing eastward to what is now part of the Black Fork. This divide was higher than 1,300 feet above tide at some distance north and south of the col. An examination of the map and study in the field shows that the Clear Fork, from a point southwest of Perrysville, flows in a valley which narrows in the direction of flow, an abnormal condition, explained only by reversal as a result of glacial damming. To the east of the col, the Clear Fork valley widens perceptibly until it reaches the junction with the Black Fork, where it is more than a quarter of a mile wide.

At this point it might be well to digress for a few moments and discuss the features of the State Park. This area outlined on the map by State Forester Edmund Secrest, is one of the most interesting from the standpoint of both Geology and scenery. It is one of the recent additions to the state forest reserve, containing a purchase area of approximately 1,500 acres, of which 850 acres have already been acquired by the state. It is the opinion of the writer that no more beautiful park area exists in Ohio. There is much to remind one of the mountain regions of the west, where below timber line occur various species of coniferous trees. Hemlocks, pines and hardwoods grace the steep sides of the narrow, canyon-like valley, through which flows the Clear Fork, a clear, swiftly flowing stream. The gorge, near the col, is a fine example of a youthful valley, about 320–340 feet deep and approximately a quarter of a mile wide across the top at its narrowest point, tapering down to a width of about 200–300 feet at the bottom. Other features of youth are the steep sides with bold rock outcrops, forming prominent cliffs, typical V-shape, overlapping spurs, swiftly flowing stream with clear water and small rapids, indicating that it is still deepening its valley. On the outside of the bends are present steep, undercut slopes with characteristic cliffs and on the inside the more gently inclined slip-off slopes. Above and below the col the valley widens and flood plain scrolls make their appearance. At the point where the Clear Fork and Black Fork meet, the valley is quite wide, possessing a flood plain of considerable breadth. The

same is true of the valley of the Clear Fork southwest of Perrysville, where the gorge begins. The youthful appearance of the valley is in harmony with the theory that a divide existed here in preglacial time through which has been cut the narrow, post-glacial gorge which lies within the boundaries of the park.

About a half mile or more west of Spellacy (Loudonville Quadrangle) there existed in preglacial time, a divide separating a tributary which flowed westward and another flowing eastward into the Mohican River. From the junction of the Clear Fork and Black Fork the Mohican River flows eastward in a valley

FIG. 3. View of the Clear Fork gorge in Mohican Park.

which narrows until it reaches the col, west of Spellacy; to the east of the col the Mohican valley widens to the south. Lake Fork, coming from the north, flows in a valley which narrows markedly until it reaches a point about three-quarters of a mile north of its junction with the Mohican River. This position marks the preglacial divide between a short tributary to the Mohican and another flowing northward into the trunk stream which flowed from Loudonville to Big Prairie and northward. The upper Lake Fork occupies, in part of its course, what appears to have been the valley of a tributary which flowed south into the trunk stream. At Loudonville a tributary, now part of Black Fork, flowed northward and joined the main stream. This tributary had other branches, one flowing east from the Clear Fork col and another flowing

west from the Spellacy col, and two others, Horsetail Run and Pine Run.

The reversion of drainage from north to south may have occurred during an invasion of the ice, earlier than the Illinoian. There appears to be no evidence of an earlier invasion than the Illinoian, but that fact does not exclude the possibility.

Leverett's map[4] shows the edge of the Illinoian drift extending northward parallel to the Mohican and a few miles east of it, disappearing beneath the Wisconsin drift to the west of the town of Nashville. The late Wisconsin drift border extends from a point near Newville to Loudonville, and south of Nashville to a position south of Millersburg and eastward. During the Illinoian glaciation the whole of the Mohican River and the area about Loudonville was covered by the ice. During the late Wisconsin the ice edge stood from Newville to a point south of Loudonville where the Lake Fork joins the Mohican River, indicating that the late Wisconsin ice did not cover the State Park portion of the Clear Fork gorge. There is a decided contrast in topography between the area covered by Illinoian drift and that covered by the later till; the cycle of erosion is farther advanced in the case of the former. In the State Park area there appears to be little evidence of late Wisconsin glaciation. Therefore it would seem that it was either during the Illinoian or an earlier epoch of glaciation that the drainage was here reversed. Between the two epochs there was much erosion. If the deep gorge in the park, at the col, was cut during and since Illinoian time it is not unreasonable to assume that many of our deep valleys in southeastern Ohio could be post-Illinoian in age. During the long interval between the Illinoian and Wisconsin glaciations the drift may have been removed from the preglacial valleys and further deepened by erosion. Coffey[5] in his paper remarks, "practically all the deep valleys in the northeast section of the state, and probably in other sections as well, are of interglacial or postglacial origin." Although the writer does not agree in full with this statement, it is clear that we must assign a great amount of erosion to interglacial time. If each advance of the ice caused changes in the drainage, it stands to reason that the present drainage lines may in some cases bear little or no relation to the drainage in preglacial and interglacial time.

[4]U. S. Geol. Survey Monograph XLI, Plate XIII.
[5]Coffey, G. Ohio Journal of Science, Vol. XXX, November, 1930, p. 374.

As the ice advanced during Illinoian time or earlier, lakes were formed between the major divide to the south and the ice to the north. The water rose until it was forced over the divide located between the towns of Millersburg and Killbuck. The broad valley of the trunk stream which leads from Perrysville to Loudonville was occupied by the glacier, blocking the drainage to the north, in consequence of which the waters were forced to take a southerly route over the divides at the State Park and at Spellacy and by way of the Mohican River. During interglacial time which followed the Illinoian the valleys were in large part cleared of their drift deposits. If the

Fig. 4. View of the col, west of Spellacy.

reversion took place in Illinoian time or earlier, the waters of the Wisconsin glacier must have passed through Clear Creek gorge. What glacial debris (outwash) has been laid down in the gorge during Wisconsin time has been largely removed. Terraces occur in the valley of the Mohican River; their elevation appears to be about 960–980 feet above sea level. The gorge of the Mohican River, before the Wisconsin epoch, in interglacial time, may have been as deep as it is at present. This would be in accordance with what is known to be true at other localities in Ohio where evidence is sufficient to prove the excavation of deep valleys in interglacial time.

During the retreat of the late Wisconsin ice, several elongate lakes were formed. These have been called the Finger Lakes of Ohio by Professor Hubbard,[6] of Oberlin. One of them, called

[6]Hubbard, George D. Ancient Finger Lakes in Ohio. Amer. Jour. of Sci., Series 4, Vol. 25, 1908.

Lake Killbuck, was formed by the damming of the Killbuck valley near Holmesville by a moraine. This lake extended northward beyond Wooster and was finally drained by the lowering of the outlet located in the morainal dam. The broad flat of the Killbuck valley with its extensive swamp lands and muck deposits represents the poorly drained floor of Lake Killbuck. Another large lake produced by glacial damming during the retreat of the Wisconsin ice extended from the broad valley at Big Prairie and Custaloga to West Salem. Morainal deposits in the valley from Lakeville to Shreve formed a very effective barrier to the exit of the lake waters. The outlet of this body of water, called Lake Craigton, was by way of Lake Fork, a tributary of the Mohican River. As the late Wisconsin ice sheet receded, recessional moraines were formed. Leverett[7] shows three distinct morainic belts extending in an east-west direction in Wayne and Holmes counties. The two southernmost ones coalesce in the vicinity of Loudonville and Nashville.

CONCLUSION.

A preglacial divide existed between Millersburg and Killbuck, shutting off the escape of the waters of the Old Mohican to the south. The only possible exit for the drainage was by way of the broad valley past Jeromesville and northward past Savannah to the Vermilion River. The width and depth of the cols and the fact that the Illinoian glacier passed over a large part of the area seems to indicate that the reversion of drainage occurred during Illinoian time or possibly earlier, although no till of earlier age is present in the region. In interglacial time the Illinoian till was largely removed from the preglacial valleys, which were probably deepened by erosion. These valleys were subsequently filled with Wisconsin till and outwash deposits.

[7]Ibid. 1, pp. 423.

THE GENUS AGALLIA—EXTERNAL CHARACTERS USED TO DISTINGUISH THE SPECIES INJURING ECONOMIC CROPS.

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The species of Agallia are primarily pests of grasses, grains, and forage crops. They are very common and abundant upon clover, alfalfa, soy beans and similar forage crops, while meadows and pastures normally support large populations. Field workers engaged in population or disease transmission studies have found it almost impossible to distinguish and determine these species occurring on economic plants with the present treatments in literature. The only previous treatment of the Genus was by Osborn and Ball in 1898[1]. At that time they illustrated three of these species and treated eight of the species included in this discussion. Since that time Baker[2] (1898) has described two and Van Duzee[3] (1909) has described one, which are treated here. In view of the fact that at the present time there is no key dealing with all of these economic species and not more than half have previously been illustrated in any way, this brief discussion is contributed to assist field workers in recognizing them. Line drawings have been included so as to illustrate the external genital characters. The character of the male genitalia, especially the size and shape of the male plates is the best external character available for separation, although the character of the posterior margin of the last ventral segment of the female is very good in several species. In a few cases the posterior margin of the female segment is quite variable.

Examination of the internal genital characters of the male show them to be very similar in closely related species. Since other workers are examining the internal genitalia with the expectation of treating all the species of the genus and in view of the fact that the external characters are adequate for separating practically all of the economic species, the internal characters are not illustrated nor described at this time. It

[1]Osborn and Ball. Proc. Dav. Acad. Sci., Vol. VII, pp. 45–64. 1898.
[2]Baker. Psyche VIII, p. 199. 1898.
[3]Van Duzee. Bul. Buf. Soc. Nat. Sci. IX, p. 210. 1909.

may be possible that through a study of these internal characters species of economic importance will be found that have not yet been described, but the internal characters examined, although differing, seem to be within the range of possible variation.

There are two rather distinct groups of species from the standpoint of distribution. One group occupying the eastern and central states and another group found almost entirely in the western mountain states and the Pacific coast. With the exception of *sanguinolenta*, which extends into the western mountain states, these two groups scarcely overlap.

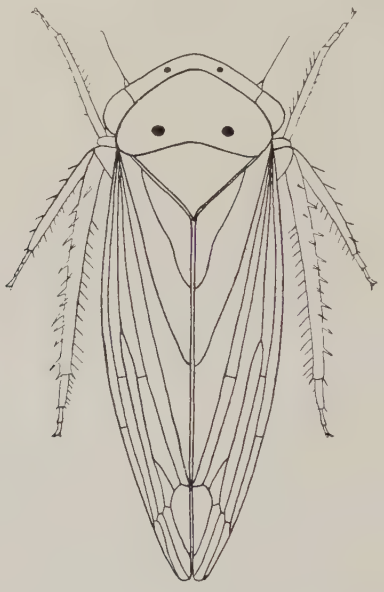


FIG. 1. *Agallia 4-punctata* Prov.
Dorsal view showing general appearance of the species of the genus.

The eastern group is composed chiefly of *sanguinolenta*, *constricta*, *4-punctata*, *novella*, *deleta* and *cinerea*. The western group is composed of *uhleri*, *californica*, *lyrata*, *bigeloviæ*, *gillettei* and partially of *sanguinolenta*. Of these species, *sanguinolenta* is the most widespread and abundant and lives upon a wide range of hosts. For many years it has been known to occur abundantly upon grains, grasses, forage crops and truck crops. It has been recognized as a pest especially of clover and alfalfa and the populations upon these crops are frequently large.

More recently rather large populations have been found on potatoes, sugar beets, beans and many other truck and field crops in varying abundance. It occurs as far west as Utah and Idaho, but its occurrence in California and other Pacific coast states is doubtful, although it has previously been recorded for California. It may be found that the insect at present called *sanguinolenta* belongs to more than one species. The writers have interpreted the large amount of material examined from the eastern and western United States as representing a quite variable species rather than two or more very closely related species. Biologic work has not been carried out to date to prove or disprove this point. Three other species in the eastern United States are frequently found with *sanguinolenta* on clover and alfalfa. These species are *novella*, *constricta*, and *4-punctata*, all of which extend as far west as Kansas and Colorado. *A. constricata* is recorded for Texas and *4-punctata* for California. There is some question concerning the authenticity of this latter record, although two specimens are at hand from Southern Idaho. Although not as abundant as *sanguinolenta*, these species have frequently been found in sufficient abundance to be of economic importance. These occur in small numbers also upon several of the truck crops and are very abundant in grasses and meadows. *A. deleta* occurs only in the southeastern United States (South Carolina, Georgia, and Florida) and may not be a species of economic importance. No economic food plants have been found or reported. *A. cinerea* is a Mississippi valley species occurring originally on native grasses and now feeding upon cultivated grasses, small grains and forage plants. It has been found as far west as Colorado and Arizona and is also recorded for California, but with a doubtful identification. Of the western species *uhleri* is most widely distributed, occurring from Iowa and Missouri to the Pacific coast, while the other species, *californica*, *lyrata* and *bigeloviæ* occur only in the Pacific coastal states and the southwest, if we may judge from available material and known records.

In California *lyrata* is found upon more crops, but usually in smaller numbers. It has been taken from 22 different crops, among which are alfalfa, sugar beets, potato, beans, carrots, and turnips. Large populations occasionally occur on sugar beets. *A. uhleri* is the most abundant species on alfalfa and the populations are quite large. It occurs on several other crops of which potato, carrots, beans and melon are the most important.

A. californica also is found abundantly upon alfalfa and occurs in greater abundance upon such crops as potato, bean, carrots, parsnip, squash and sugar beets. *A. bigeloviæ* occurs only occasionally upon economic crops.

KEY TO THE SPECIES AGALLIA ATTACKING ECONOMIC CROPS.

A. Posterior portion of pronotum with two round black spots. Large, robust or rather long and wedge-shaped.
  B. Broad (almost 2 mm.) and robust; female segment almost truncate posteriorly, male plates short and narrow.....*4-punctata*
  BB. Much narrower, wedge-shaped, female segment deeply emarginate or strongly produced, male plates longer and broader.
    C. Posterior margin of vertex regularly curved, female segment suddenly constricted near the middle then strongly roundingly produced, male plates rather long bluntly rounded.....*constricta*
    CC. Posterior margin of vertex produced anteriorly at the middle, female segment deeply roundingly emarginate, male plates broad, bluntly rounded, fitting into a box formed by apices of pygophers.....*novella*
AA. Spots if present on anterior portion of pronotum or markings longitudinal in general form. Species usually short and robust.
  D. Female segment with long pointed inwardly projecting lateral angles or with four rather prominent lobes, male plates lyrate or greatly elongate.
    E. Apical half of female segment narrowed about one-fourth entire width forming inwardly set, long pointed lateral angles. Male plates long and narrow.....*gillettei*
  EE. Female segment not narrowed apically and with a four-lobed condition, male plates lyrate or elongate.
    F. Female lobes conspicuous, separated by deep and rather broad incisions; male plates long and narrow.....*bigeloviæ*
    FF. Female lobes rather short, separated by broad shallow indentations, male plates convexly then concavely curved to truncate tips forming lyre-like structures.....*lyrata*
  DD. Female segment sinuate or notched, but without conspicuous lobes. Male plates neither lyrate nor greatly elongate.
    G. Female segment shallowly roundingly emarginate with a minute tooth at middle, male plates short but strongly narrowed to narrow, but blunt tips.....*deleta*
    GG. Female segment truncate or slightly notched at middle, male plates rather broad at apex, not strongly narrowed.
      H. Female segment shallowly emarginate and slightly notched at middle, male plates most strongly produced on outer angles.....*uhleri*
      HH. Female segment truncate or produced and notched at middle, male plates more strongly produced on middle line.
        I. Female segment truncate and rather strongly notched at middle, male plates shorter than combined width at base, apices broad and bluntly rounded.....*californica*
        II. Female segment slightly produced between lateral angles, male plates longer.
          J. Male plates narrowed from base to form broad, bluntly rounded tips.....*sanguinolenta*
          JJ. Male plates with outer margins almost straight. Posterior margins sloping obliquely to produced inner margins.....*cinerea*

Agallia 4-punctata (Prov.)

Bythoscopus 4-punctata. Prov. Nat. Can. IV, p. 376, 1872.

Easily distinguished from the other eastern species by the broader more robust form and the genitalia. Length, 4 mm. Last ventral segment of female with posterior margin shallowly concavely rounded. Male valve large, broad. Plates rather short and broad, triangular, apices rather blunt. Plates slightly longer than combined width at base.

Known to occur rather generally throughout the eastern United States and recorded for Iowa, Kansas, Nebraska, Arkansas, Colorado and California. In addition two specimens are at hand collected in southern Idaho during the summer of 1930. If it occurs in California the species is apparently very scarce.

Agallia constricta V. D.

Agallia constricta V. D. Can. Ent. XXVI, p. 90, 1894.

Resembling *novella* in form and appearance, but without the intermittent dark and light markings along the sutural line. Length, 3.5–4 mm.

Female last ventral segment long, sides almost parallel margined, abruptly constricted at about half its length. The median line carinate and the posterior margin strongly produced and obtusely rounded. Male valve about twice as broad as long, plates long and narrow, slightly constricted about middle then again widening and produced to the rounded tips.

Ranking second in abundance to *sanguinolenta* in the eastern United States. Also recorded for Kansas, Missouri, and eastern Texas.

Agallia novella (Say).

Jassus novella Say. Jl. Acad. Nat. Sci. Phila. VI, p. 309, 1831.

Resembling *constricta* in size and general form, but easily distinguished from it by the elevated and anteriorly produced posterior margin of the vertex and the dark interruptions on the sutural line of the wings. Length, 3.75 mm.

Female last ventral segment with lateral angles long, well produced, posterior margin roundedly excavated from the lateral angles more than half way to the base. Male valve short, truncated, plates long, rather blunt at tips. Pygophers rather large, convexly inflated, forming an almost square opening posteriorly into which the plates fit like a lid.

A common species in the eastern United States and recorded for Kansas, Missouri, Colorado and Vancouver Island.

Agallia gillettei Osb. and Ball.

Agallia gillettei Osb. and Ball. Proc. Dav. Acad. Sci. VII, p. 60, 1898.

Usually narrower than *sanguinolenta*. Length, 2.75–3 mm.

Female last ventral segment narrowed about one-fourth the width of posterior half, forming prominent, rather pointed posterior angles. Between these the posterior margin is excavated by three rather abrupt, successive steps. The median notch at the apex reaches over half way to the base of the segment. Male valve twice wider than long, plates almost three times as long as valve, margins rolled up, giving them a cylindrical appearance and which causes them to appear narrow. The ends of the plates upturned.

Although *gillettei* is usually not of importance economically, it occurs through the southwest on native vegetation. It is interesting to note that specimens were collected in Florida on Sanibel Island, in April, 1921, by the senior author. This adds greatly to the known range of this species.

Agallia bigeloviæ Bak.

Agallia bigeloviæ Baker. Psyche VII, Suppl. 1, p. 26, 1896.

Resembling *lyrata* in general appearance, but easily distinguished by the genitalia of both sexes. Length, 3 mm.

Last ventral segment of female short and broad, posterior margin consisting of four prominent rounding lobes, the incisions between them reaching more than half way to the base. Male valve short and narrow, plates long and narrow, slightly constricted at base and with apices laterally compressed.

Specimens have been collected in California, Colorado, New Mexico and Arizona.

Agallia lyrata Bak.

Agallia lyrata Baker. Psyche VIII, p. 199, 1898.

Form and general appearance of *sanguinolenta*, but slightly larger. Length, 3.5 mm.

Female last ventral segment rather short and broad, lateral margins roundingly produced, posterior margin formed into four distinct, but rather shallow lobes. A V-shaped notch at the middle separates the two inner lobes and a shallow rounding emargination either side separates the outer from the inner lobes. Male valve short and broad, plates strongly roundedly widened at base, then concavely rounded to broad blunt apices which are upturned and slightly wider at tips. Together these give the appearance of a lyre.

Records at present are from California and Vancouver Island only.

Agallia deleta V. D.

Agallia deleta V. D. Bul. Buf. Soc. Nat. Sci. IX, p. 210, 1909.

General form of *sanguinolenta*, but slightly smaller and without dark markings. Length, 2.5–3 mm.

Female last ventral segment with posterior margin slightly concave with a very minute tooth at middle. Male valve rather long and broad, plates as broad as valve at base, gradually tapering to rather blunt apices.

Known only from the southeastern United States. Recorded for Florida, South Carolina, and Georgia.

Agallia uhleri V. D.

Agallia uhleri V. D. Can. Ent. XXVI, p. 91, 1894.

A little longer than *sanguinolenta* and less robust, but similar in color and general appearance. Length, 3–3.25 mm.

Female last ventral segment about three-fourths as long as basal width. Posterior margin sloping from prominent angles to form a central deep triangular notch reaching about one-third the distance to the base. Male valve short, truncate posteriorly, plates longer than combined width at base, lateral margins tapered to blunt apices which are slightly obliquely truncate, the outer angles longer than inner margins, tips usually dark margined.

A typically western species occurring from Iowa and Missouri to California.

Agallia californica Baker.

Agallia californica Baker. Psyche VIII, p. 199, 1898.

Resembling *sanguinolenta* in size and appearance, but with female segment more deeply notched and male plates shorter and more truncate. Length, 3–3.25 mm. Markings as in *sanguinolenta*.

Female last ventral segment more than twice as broad as long with a distinct notch at center extending about one-third the distance to base. Male valve very short and broad, truncate, plates a little shorter than combined width, apices truncate, outer margins rather strongly produced and not narrowed toward apex. Inner margins with a very slight tooth at apex either side of median line.

Recorded only for California.

Agallia sanguinolenta (Prov.)

Bythoscopus sanguinolenta Prov. Nat. Can. IV, p. 376, 1872.

This is the most common and widespread species of the genus and probably is of more importance economically, although there is a possi-

bility that it may be confused with other closely related, but undescribed, species. Length, 3 mm.

Female segment somewhat variable. Usually slightly sinuate and with a weakly produced lobe either side of a shallow median notch. Male valve short, almost truncate, plates broad, truncate at apex, one-half longer than wide.

Probably the most widely distributed of all the species of the genus. It occurs abundantly throughout the eastern United States and has been recorded generally throughout the western United States to California. The identity of the species is the most important question in regard to these records of distribution.

Agallia cinerea Osb. and Ball.

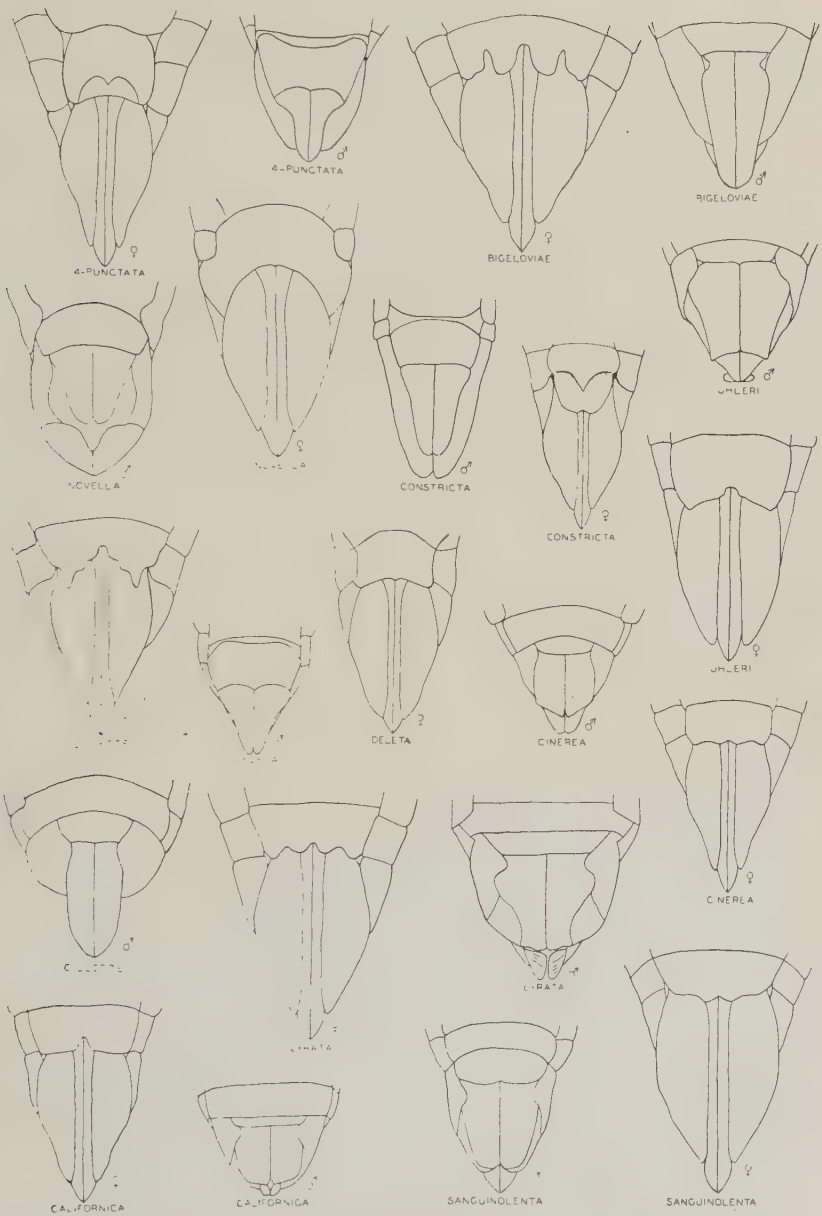
Agallia cinerea Osb. and Ball. Proc. Dav. Acad. Sci. VII, p. 62, 1898.

Resembling *sanguinolenta* in size and structures, but pale cinereous in color and with distinct male genitalia. Length, 2.5 mm.

Female last ventral segment short and broad, shorter than in *sanguinolenta*. Posterior angles produced and rather prominent. Posterior margin slightly sinuated and faintly notched at middle. A transparent portion extending almost to base permits the ovipositor to be visible through the segment and causes it to appear deeply notched. Male valve short and broad, truncated or slightly concavely rounding. Plates about as long as combined width, outer margins almost straight, posterior margins sloping from rather prominent angles to inner margins which are slightly divergent and pointed.

The female genitalia are very similar to *sanguinolenta*, but the males of the two species are quite different and easily distinguished.

Chiefly a Mississippi valley species. Recorded for Tennessee, Iowa, Kansas, Colorado, Arizona, and California. If it occurs in the southwest and California it is very rare.



External genital characters of the species of the genus Agallia which are of economic importance.

THE ALIMENTARY CANAL OF ASAPHES MEMNONIUS HBST.

JOHN T. BIGHAM.

INTRODUCTION.

The material used in this work was collected by Dr. C. H. Kennedy at the Franz Theodore Stone Laboratory on Lake Erie, during the summer of 1929. The beetles were found feeding on watermelon rinds scattered in the forest. A considerable number of specimens were fixed in Kahle's Fixative, after which they were transferred to and preserved in 70% alcohol.

This species of click beetle is pale brown in color with paler legs. It varies in length from 13–26 mm. According to Horn it occurs from Canada to Georgia and westward to Colorado.

The author wishes to extend his thanks to Dr. Kennedy for the use of this material and also for helpful suggestions and criticisms during the progress of the work. He also wishes to acknowledge the help of Prof. J. S. Hine in determining the species.

Gross Anatomy of the Digestive Tract.

General Discussion.

In insects the alimentary canal is divided morphologically into three primary regions on the basis of embryonic origin. The fore-intestine (stomodaeum) arises as an invagination of the ectoderm at the anterior end. The hind-intestine (proctodeum) arises as a similar posterior invagination. Connecting these two regions is the mid-intestine (mesenteron) which is derived from endodermal tissue. In correlation with the external epithelium the epithelial lining of the fore and hind intestines secretes chitin, which is found lining these two regions as a definite membrane.

The alimentary canal of *Asaphes memnonius* is of medium length as is usual in insects of phytophagus habit. In the region of the thorax it is incased by large wing and leg muscles. In other regions it is supported by tracheae and by suspensory muscles attached to the body wall.

Gross Structure of the Fore-Intestine.

In *Asaphes memnonius* the fore-intestine is very short. It extends from the mouth through the head capsule into the anterior part of the prothorax and comprises about one-thirteenth of the total length of the alimentary canal. It consists of two main divisions—*the pharynx* and *the crop.*

The pharynx begins at the mouth and comprises nearly the first half of the fore-intestine. In most specimens it appears as a narrow, nearly cylindrical tube, though in some specimens it is somewhat dilated. It has attached to it muscle strands which radiate out from it in various directions and are attached to the interior surface of the head capsule.

The crop varies considerably in size in different specimens. In some specimens there is no very distinct external line of demarcation between the pharynx and the crop. The crop continues on for some distance as a narrow tube of about the same diameter as the pharynx. Just before joining the mid-intestine it enlarges into a small bulb-like structure. In other specimens there is a constriction at the point of union of pharynx and crop and the crop begins to enlarge immediately and forms a sack two or three times as large as that in the specimens first mentioned. Since there is this variation in size, the crop apparently serves to some extent as a reservoir for food.

The Oesophageal valve marks the separation between the fore- and mid-intestine. The posterior end of the bulb-like crop disappears into the larger anterior end of the mid-intestine.

Gross Structure of the Mid-Intestine.

The mid-intestine is commonly known as the stomach. In this insect it is relatively long, extending from the anterior part of the prothorax to about the beginning of the third abdominal segment, and comprises approximately one-half the entire length of the alimentary canal.

It has a rather peculiar shape. The anterior portion lying in the prothorax and metathorax may be compared in shape to that of a club. The large end of the club is at the anterior end where it joins the fore-intestine. This enlarged end is somewhat flattened dorsoventrally, and it has shallow coeca which project forward on either side of and also dorsal to the posterior end of the crop. The number and position of these coeca seems to vary in different specimens. Following this enlarged anterior portion the stomach grows narrower and before it enters the mesothorax has become a narrow cylindrical tube. This tubular portion traverses the mesothorax. In the metathorax the stomach begins to enlarge again and forms a large pear-shaped sack which frequently occupies the larger part of the body cavity in this region. The shape of this enlarged posterior portion may be compared more exactly to that of a punching-bag used in gymnasiums. This enlarged portion extends into the second abdominal segment where it narrows abruptly, and the stomach once again becomes a tube which tapers towards its union with the hind-intestine at the pyloric valve, located at about the division between the second and third abdominal segments. The pear-shaped posterior enlargement of the stomach varies considerably in size and the tubular portions, both anterior and posterior to it, are correspondingly longer and shorter.

The surface of the stomach is covered with minute pimples which prove to be cell nests or nidi which project in part through the muscle layers of the stomach wall.

Gross Structure of the Hind-Intestine.

The hind-intestine comprises nearly one-half the total length of the tract. Its anterior limit is marked by the attachment of the malpighian tubules. It extends from this point to the anus.

The malpighian tubules are four in number and are attached at four different points around the circumference of the digestive canal, those on the two sides being slightly nearer together. They appear as long convoluted tubes which lie in the body cavity along the digestive tract. A few loops extend forward for a short distance to the pear-shaped portion of the stomach, but for the most part they run back and forth along the hind-intestine, in many places adhering to the walls of the intestine but not attached directly to it.

The pyloric valve lies just posterior to the attachment of the malpighian tubules. In this insect the pyloric valve is an unusually long structure occupying a section of the intestine which is about one-eighteenth of the total length of the hind-intestine.

The hind-intestine at the point where it joins the stomach is of the same diameter as the end of the stomach, but it immediately tapers down to form a narrow tube which makes a rather sharp bend to the right. This entire section of the intestine makes up the pyloric valve. From this point on the intestine has no very sharp divisions. The walls are very thin and the size and shape of different portions varies considerably, depending upon the amount and position of the food material contained.

At the end of the pyloric valve the intestine enlarges rather abruptly and extends cephalad to about the end of the first abdominal segment. Here it turns back again, thus forming a loop. The position in which this loop lies varies somewhat. The position shown in Fig. 1 is diagrammatic. It is usually not so wide a loop as this and often lies in such a position as to hide the pyloric valve. The portion of the intestine comprising the first half of this loop is usually comparatively narrow and the walls appear to have constrictions at more or less regular intervals. From the forward end of the loop back to the last segment of the abdomen the intestine is usually distended with food material and no constrictions are apparent. The walls of the intestine, especially in the dilated portion are very thin and are semi-transparent. When examined under a binocular, white muscle strands can be seen running longitudinally along the intestinal walls. In a few of the specimens examined the intestine was empty and appeared as a tube of about the same diameter from the pyloric valve to the last segment of the abdomen.

In the last abdominal segment the intestine becomes very much narrower and extends to the anus as a very narrow tube. Fig. 1 represents a female specimen. In the male specimens which were examined this portion of the intestine did not appear to be so narrow.

Histological Structure of the Alimentary Canal.

Histological Structure of the Fore-Intestine.

Although divided into two divisions, pharynx and crop, the fore-intestine reveals a uniformity of histological structure throughout its

length. The following layers of tissue from within outwards can be clearly demonstrated in its walls: (1) a primary intima, (2) a secondary intima, (3) an epithelium of hypodermal cells, (4) a layer of longitudinal muscles, and (5) a layer of circular muscles.

The intima is composed of chitin and is homologous with the cuticula of the body wall. It is a non-cellular, almost transparent layer and is secreted by the hypodermal epithelium. In the pharynx the two layers of the intima are fairly distinct. The primary intima stains darker but has a clear uniform structure. The secondary intima does not stain as dark and appears to have a granular structure. The intima of the pharynx is of nearly uniform thickness and presents a smooth even surface toward the lumen of the intestine. There are no spines present. In cross-sections of this region the intima is seen to be thrown up into several large folds.

In the crop the two layers of the intima are not very clearly differentiated. The division between them can be seen in some phases as an indistinct wavy line, the primary intima being relatively thinner than in the pharynx. The intima in the region of the crop is also much more irregular in appearance than in the pharynx. The side toward the lumen of the intestine presents a rough uneven appearance and in some places bears spines which are often long and needle-like. These spines are longer and more numerous near the esophagial valve. They seem to be distributed irregularly. In the narrow anterior portion of the crop the intima is thrown into numerous folds which nearly fill the lumen of the intestine. Where the crop is distended there are only a few small folds distributed at intervals.

The epithelium of the fore-intestine is a thin layer composed of irregular shaped cells. It is thrown into folds following the folds of the intima. In stained sections a continuous purple line can be seen along the edge of the epithelium on the side next the intima. The nature of this dark band is uncertain. The epithelial cells in most places are flattened and are much longer than thick, but in some places especially where the epithelium forms a fold they are cuboidal in shape.

In the crop the epithelium is even thinner than in the pharynx. In sections the epithelium appears in many places as a thin string with enlargements at intervals. One or more nuclei can be seen in most of these enlargements. The limits of the individual cells cannot usually be clearly distinguished except in the places where the cells are cuboidal in shape.

No basement membrane can be distinguished apart from the epithelial layer.

The logitudinal muscle layer of the fore-intestine is a continuous solid layer made up of a great number of bundles of muscle fibers. Nuclei are seen in many of the bundles, and are usually situated on the edges of the bundles as seen in cross-sections.

The circular muscle layer is a little thicker than the logitudinal layer. It is made up of rather thick muscle bands. Frequently there are three or four of these muscle bands running alongside each other. Numerous nuclei can be seen. They are often strung out in rows of four or five nuclei running lengthwise of the muscle. In longitudinal sections

of specimens in which the crop is of nearly uniform diameter throughout its length the circular muscle layer becomes thicker as it nears the oesophageal valve. Where the crop is distended the muscle layers are much thinner than otherwise.

In longitudinal sections in which the crop is distended up to the point where it joins the pharynx, the pharynx appears to project slightly into the lumen of the crop.

No "peritoneal membrane" was observed.

Histological Structure of the Oesophageal Valve.

The oesophageal valve marks the point of junction of the fore- and mid-intestine. Just anterior to the stomach the walls of the fore-intestine become constricted. Then they project into the lumen of the stomach, turn back upon themselves, and unite with the walls of the stomach.

The intima as it enters the constricted portion of the valve becomes smooth and regular in appearance. It passes into the stomach, turns back around the projecting lobe of epithelium and disappears between the lobe of fore-intestinal epithelium and the first group of stomach cells.

As the fore-intestinal epithelium enters the constricted portion of the valve its cells become distinctly cuboidal in shape. As it enters the stomach and turns back upon itself the cells become columnar in shape. Just after it makes the turn the cells become extremely long and narrow and appear closely packed together. A cleft usually appears between the last of these epithelial cells and the first of the stomach cells.

Longitudinal muscles are not especially abundant in the region of the valve. In some longitudinal sections the ends of the large longitudinal muscles of the stomach can be seen extending into the constricted portion of the valve.

The circular muscle layer of the fore-intestine becomes thicker just anterior to the valve and passing into the constriction at the valve it nearly fills that constriction with large masses of circular muscle bundles which by their contraction serve to close the valve.

At the oesophageal valve the muscle layers reverse their positions in respect to each other. Anterior to the valve the circular muscles are outside the longitudinal muscles, posterior to the valve the reverse is true.

Histological Structure of the Mid-Intestine.

The mid-intestine extends from the oesophageal valve to the pyloric valve. A histological examination of the stomach wall gives the following sequence of tissues from within out; (1) an epithelium of endoderm cells, (2) circular muscles, (3) longitudinal muscles. A basement membrane can probably be seen in some places at the base of the epithelial cells. No "peritoneal membrane" has been observed. The structure of the stomach wall appears to be about the same throughout its length although the diameter of cross-sections taken from its various portions varies greatly.

The appearance of the epithelial layer varies with the different stages in the process of secretion. The cells are columnar shaped but are much longer at some times than at others. Sometimes the cells form a single layer but usually they are built up into papillæ. Sometimes these papillæ become very tall and nearly touch one another on their sides. This is especially noticeable in the narrow portion of the stomach. Nidi or "cell nests" appear at regular intervals and are conspicuous objects since they stain darkly. These are nests of embryonic tissue from which new cells arise. They lie below the rest of the epithelium and project in part through the muscle walls. Since there is usually a papilla standing up between each two nidi, each nidus appears to be situated at the bottom of a pit.

Both merocrine and holocrine types of secretion seem to be carried on. In some cross-sections the food material in the intestine is seen to be completely surrounded with a ring of little globules of digestive secretion. These globules can be seen issuing from the ends of the epithelial cells. Apparently the cells rupture at their ends and the fluid secretion contained in the extremity of each cell flows out forming a globule as it enters the lumen of the intestine. The cell wall at this emptied end then shrinks and becomes wrinkled and shrivelled in appearance. This gives the ends of the cells a striated appearance. At an apparently later stage the cells are seen to be tipped with filaments which are probably the frayed out walls of the cell ends which have just been described. Among the cells of this second stage can be seen some which show at their tips a convex surface within the filaments. This probably is the surface of new secretion which is welling up from the body of protoplasm below. This second secretion is thrown off much as in the first case. Apparently this process repeats itself as many as two or three times. In the first stage the cells formed a single layer. In the mean time they have been building up and forming papillæ. The nuclei gradually move out towards the tips of the cells and finally the entire mass of cells breaks down in the form of holocrine secretion. This latter process was plainly taking place in many of the sections which were examined. New cells then grow out from the nidi and replace the old ones.

The process which has just been described as the probable method of secretion in this insect was suggested to the author by Dr. C. H. Kennedy.

Just outside the epithelial layer are large circular muscle bundles. These bundles are more or less isolated and do not usually form a continuous layer. In some places, however, their ends overlap and they appear in cross-section as a nearly continuous ring around the epithelium.

Outside the circular muscles are the longitudinal muscles. These also occur as isolated bundles, thirty or forty or more of them being seen in a cross-section. Frequently several of these bundles are seen grouped together.

Between the epithelial layer and the circular muscles especially within folds of the epithelium, fine strands of tissue appear which are probably tracheoles. In such places there can be seen also apparently isolated nuclei. The nature of these is uncertain.

Histological Structure of the Hind-Intestine.

The malpighian tubules arise as outpocketings of the hind-intestine. In *Asaphes memnonius* they join the digestive tract just at the point of junction of the mid- and hind-intestine. The epithelium just anterior to the insertion of these tubules is composed of typical stomach cells while the epithelium immediately posterior to their insertion is covered with a thin layer of chitin which shows that it belongs to the hind-intestine.

The epithelial cells of the tubules are very irregular both in shape and size. Their irregular shape gives the lumen of the tube a very irregular outline. Frequently two large cells will have very small cells inserted between them. The nuclei are large and usually ovate in shape. The tubules are lined with a striated border. This border looks as if it were made up of a dense lining of fine filaments extending out from the epithelial cells and with a comparatively few longer filaments extending out beyond the tips of the others.

At the origin of the tubules the epithelial cells appear crowded together and columnar in shape. Progressing distally from the basal end of the tubule the cells gradually assume their more characteristic appearance.

On the outside the Malpighian tubules are bounded by a narrow layer of connective tissue containing many nuclei.

The pyloric valve is situated just posterior to the point of insertion of the malpighian tubules. In *Asaphes memnonius* this valve is an unusually long structure occupying the entire length of the first bend in the hind-intestine.

Immediately posterior to the insertion of the malpighian tubules the epithelial layer is thrown into a number of folds surrounding the lumen of the valve. The cells making up these folds are long and columnar shaped. As the epithelial layer passes from this point into the constricted portion of the valve the cells become cuboidal and finally small and irregular in shape, giving the epithelial layer somewhat the same appearance as the fore-intestinal epithelium. Throughout the constricted portion of the valve the epithelium is thrown into long folds running lengthwise of the valve. Near the posterior end of the valve where it is usually tightly constricted these folds practically obliterate the lumen of the valve. The epithelial layer is covered with an intima of chitin. The intima is very thin at the anterior end of the valve but becomes thicker toward the posterior end. At the point where the pyloric valve ends and is followed by a wider portion of the intestine the cells of the epithelium become much larger and assume rather suddenly the characteristic cuboidal shape of the cells of the hind-intestine. The end of the valve frequently projects slightly into the lumen of this portion of the intestine.

The pyloric valve is surrounded for its entire length by a conspicuous layer of circular muscles, and there is an especially dense mass of these muscles at the point where the valve makes a bend. Evidently the muscles serve to close the valve at this point.

Longitudinal muscles are found both outside and inside the circular muscle layer.

The hind-intestine proper begins at the end of the pyloric valve and extends to the anus. The intestinal walls throughout this region show a close similarity of structure. The tissues are arranged in the following manner: (1) an inner intima of chitin, (2) an epithelial layer, (3) circular muscles, and (4) longitudinal muscles. In a few longitudinal sections taken from the anterior part of the hind-intestine there appeared to be some circular muscle bundles outside the longitudinal muscles.

As was mentioned in the description of the gross structure, the hind-intestine proper appears externally to be divided into three regions, a narrow convoluted anterior portion, an enlarged median portion, and a narrow posterior portion. Although differing in diameter these regions do not appear to be greatly different in morphological structure. The walls of the anterior portion appear to be constricted. The epithelium is thrown up into folds as seen in both longitudinal and cross-sections. The epithelium of the narrow posterior portion is convoluted also. In the enlarged median portion the walls appear to be stretched and no convolutions appear. In some specimens in which the digestive tract was empty the hind-intestine appeared as a tube of nearly uniform diameter throughout its length. However, it appears that the median portion is the largest portion aside from the fact that its walls are usually distended.

The intima of the hind intestine is a thin layer of chitin adhering closely to the epithelial layer.

The epithelial layer is composed of cells which are usually columnar shaped although they are comparatively short and thick and many of them would be described as cuboidal. The nuclei are comparatively large ovate structures situated usually nearer the basal portion of the cells. When stained with eosin the outer ends of the cells stain darker than their basal portions. This gives the appearance of a dark band along the side of the epithelium next the lumen of the intestine. In places this band appears somewhat striated.

The circular muscles are found immediately surrounding the epithelium. They are numerous but do not usually form a solid layer. In places where the intestine is constricted there will be frequently two or three of these muscle bands running alongside each other.

The longitudinal muscles are outside the circular muscles. They are larger than the circular muscles but not so numerous. In cross-sections they appear in groups scattered around the circumference of the section.

Where the epithelium is convoluted, both longitudinal and circular muscles are found running up into the folds in some places.

The muscles are striated as are all insect muscles. When they are contracted their edges have a beaded appearance.

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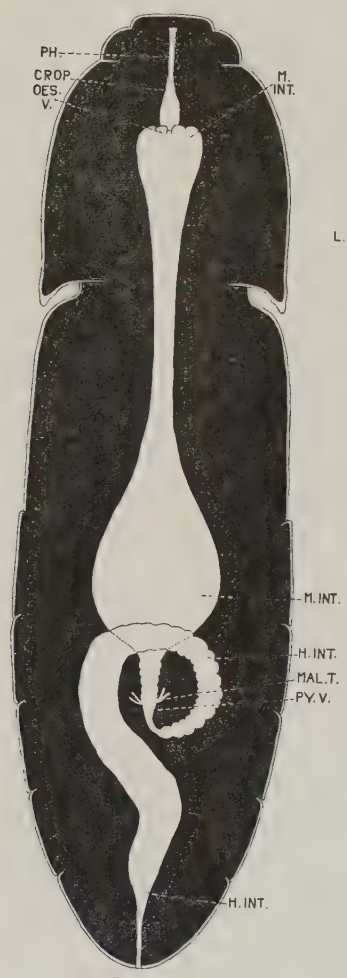

FIG. 1.

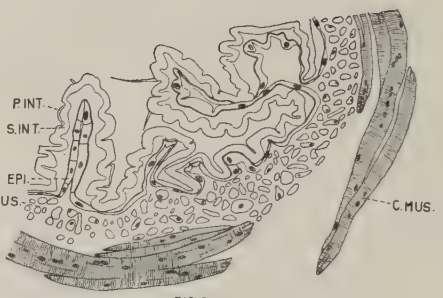

FIG 2

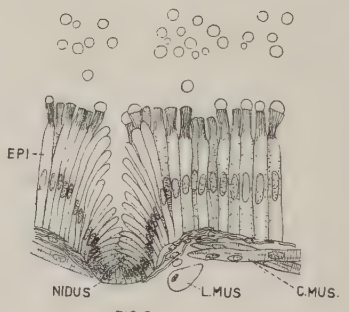

FIG. 3

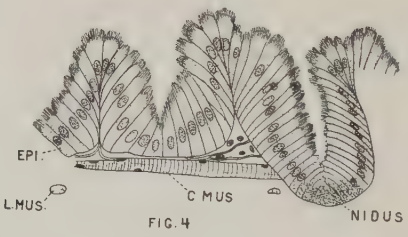

FIG. 4

Fig. 1. A dorsal view of the alimentary canal of *Asaphes memnonius*.
Fig. 2. Cross-section through constricted anterior portion of crop.
Fig. 3. Cross-section through mid-intestine showing "first stage" in the process of secretion.
Fig. 4. Cross-section through mid-intestine showing a later stage in the process of secretion.

KEY TO ABBREVIATIONS.

C. Mus.—Circular muscles.
Epi.—Epithelium.
H. Int.—Hind-intestine.
Int.—Intima.
L. Mus.—Longitudinal muscles.
Mal. T.—Malpighian tubule.
M. Int.—Mid-intestine.
Oes.—Oesophagus.
Oes. V.—Oesophageal valve.
Peri. mem.—Peritoneal membrane.
P. Mem.—Peritoneal membrane.
Ph.—Pharynx.
P. Int.—Primary intima.
Py. V.—Pyloric valve.
S. Int.—Secondary intima.

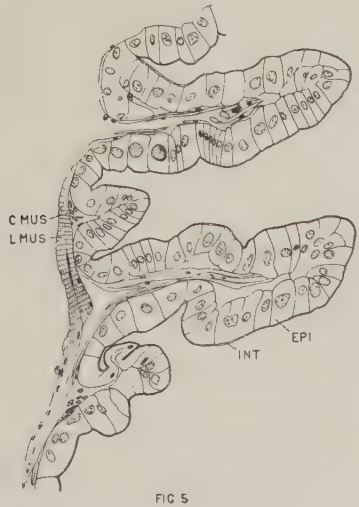

FIG 5

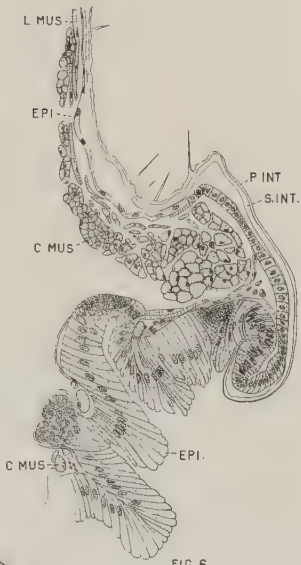

FIG. 6.

FIG. 8.

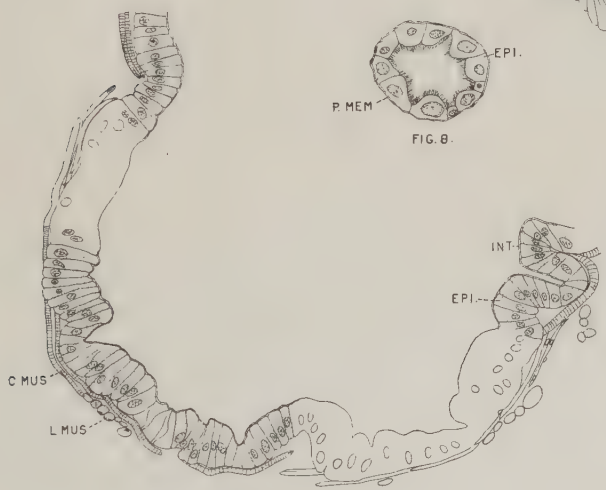

FIG. 7

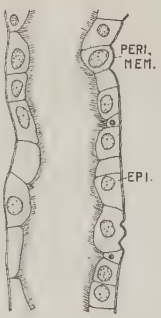

FIG. 9.

Fig. 5. Longitudinal section through anterior convoluted portion of hind-intestine.
Fig. 6. Longitudinal section through oesophageal valve.
Fig. 7. Cross-section through posterior portion of hind-intestine.
Fig. 8. Cross-section of Malpighian tubule.
Fig. 9. Longitudinal section through Malpighian tubule.

NOTE: Figures 5, 6 and 7 are magnified approximately five-eighths as much as the other histological figures.

THE ALIMENTARY CANAL OF CRIOCERUS ASPARAGI LINN.

RALPH HOWARD DAVIDSON.

INTRODUCTION.

The common asparagus beetle (*Criocerus asparagi* L.) is a phytophagus insect pest of asparagus. It is widely distributed throughout the truck-growing areas of the United States.

The study that follows was made upon the suggestion of Dr. Rodney Cecil of the U. S. Bureau of Entomology, and was begun in a course in entomology at the Ohio State University, given by Dr. C. H. Kennedy on "The Morphology and Development of Insects."

The material used was collected at Geneva, New York. The beetles were opened and fixed in Kahle's solution for 24 hours, and preserved in 70% alcohol.

The author wishes to express his appreciation for the helpful suggestions and criticisms of Dr. C. H. Kennedy, under whose direction this study was made.

Gross Anatomy of the Digestive Tract.

General Anatomy.

The alimentary canal consists of a simple tube with but few convolutions, which is characteristic of phytophagus insects. The canal is approximately one and one-fourth times the length of the insect's body. Morphologically the canal is divisible into three primary regions according to their embryonic origin. The fore-intestine (Stomodaeum) arises as an anterior ectodermal invagination; the hind-intestine (Proctodaeum) arises as a similar posterior invagination; the mid-intestine (Mesenteron or Ventriculus) which connects the two, develops as an endodermal sac from a proliferation of rings of endodermal cells, one around the posterior end of the fore-intestine and the other around the anterior end of the hind-intestine. The relation of these parts to each other is shown in Fig. 6, Plate I.

Fore-Intestine.

The fore-intestine is a short slender tube which consists of the following regions: pharynx, oesophagus, crop, and oesophageal valve.

The pharynx is the slight enlargement of the fore-intestine just posterior to the mouth which connects the mouth with the oesophagus.

The oesophagus is a very short narrow tube connecting the pharynx with the crop. It is located in the anterior part of the prothorax, and

increases slightly in size in the posterior part of the prothorax. This enlargement is the only indication of a crop being present.

The crop, as just stated, is represented by a slight enlargment of the posterior part of the oesophagus. The variation in the size of this structure is probably due to the amount of food material it contained at the time the insect was killed. This portion of the canal lies in the prothoracic segment.

The oesophageal valve is well developed and marks the division between the fore-intestine and mid-intestine by a slight constriction. This constriction is found near the junction of the prothoracic and mesothoracic segments.

No salivary glands were found.

Mid-Intestine.

The mid-intestine forms the largest part of the alimentary tract. It is marked at its anterior end by the oesophageal valve, located near the anterior part of the mesothoracic segment, and at the posterior end by the pyloric valve and Malpighian tubules located in the seventh abdominal segment. The size of the mid-intestine or stomach varies with the different specimens dissected. This is apparently due to the different amounts of food material each stomach contained. The anterior part of the mid-intestine is usually small, and the mid- and posterior parts are large in size. (Fig. 6, Plate I). Correlated with these two regions of the stomach is a slight differentiation of the epithelial lining.

Hind-Intestine.

The hind-intestine is made up of the following regions, pyloric valve, Malpighian tubules, ileum, colon, and rectum.

The pyloric valve is recognized by the constriction at the posterior end of the mid-intestine. It is located just anterior to the attachment of the Malpighian tubules to the ileum.

The Malpighian tubules are six in number and are divisible into two groups; the first group consisting of four tubules and the second of two tubules. The first group arises from a knob-like projection of the ileum just posterior to the pyloric valve, while the second arises as an evagination slightly anterior to the first group, in the region of the epithelium of the pyloric valve.

In the gross dissection the tubules are found to be entirely distinct from the walls of the canal, except near their distal ends where they penetrate the peritoneal layer of the colon. The approximate course of the tubules to the point where they enter the peritoneal layer, is shown very diagrammatically in Fig. 6, Plate I.

The vessels of the first group run cephalad, two on the dorsal side and two on the ventral side of the alimentary canal. They are embedded in the adipose tissue and follow the digestive tract in a more or less irregular or wavy path throughout most of its length. They extend forward as far as the crop and here turn caudad and follow the mid-intestine rather closely to its posterior end. At this point they leave the mid-intestine and follow an irregular course through the

fatty tissue and the body cavity in the region of the pyloric valve. Finally two tubules from the first group unite at their distal ends, forming a common stem on the dorsal side near the anterior part of the colon. Immediately posterior to the union of these two tubules one of the tubules of the second group joins this same stem, forming a common duct. This formation of a common duct is quite similar to that described for Halitica bimarginata Say (Woods, 1916). The three remaining tubules form a similar grouping on the ventral side of the colon.

The two tubules which make up the second group are smaller in size and shorter in length than those of the first. They follow an irregular course in the body cavity, being closely associated with the ileum and colon, finally each uniting with one of the common stems as described in the preceding paragraph.

These two common stems, one dorsal and the other ventral, enter the peritoneal membrane of the colon and immediately separate into the six original Malpighian tubules. They follow a straight path a short distance and gradually increase in size, becoming flattened and convoluted in shape as they approach the posterior end of the colon. They do not branch but simply follow a very irregular course (Fig. 6, Plate I), bending and folding back on themselves until the posterior part of the colon is almost completely covered with a mass of convoluted Malpighian tubules. The tubules terminate blindly at the junction of the colon and rectum.

The ileum, frequently called the small intestine, is a small tube which connects the stomach with the colon. It extends posteriorly to about the ninth abdominal segment, and then turns sharply cephalad joining the colon in the seventh abdominal segment.

The colon connects the ileum with the rectum. At its anterior end it is almost the same size as the ileum but gradually increases in size posteriorly, reaching its maximum diameter just before the junction with the rectum.

The rectum is short and heavily muscled, and is of the same diameter as the oesophagus, as shown by sections of this area. It connects the colon with the anus.

Histology of the Alimentary Canal.

Fore-Intestine.

The histological examination of the fore-intestine did not reveal any unusual structures. It is lined throughout with a rather heavy layer of chitin or intima. This layer is non-cellular and almost transparent, and is very difficult to stain. It projects into the lumen of the pharynx and oesophagus in irregular wave-like folds. As the oesophagus (Fig. 1, Plate I) gradually enlarges to form the crop (Fig. 2, Plate I), these folds become less pronounced.

The epithelium forms a single layer of rather flattened, irregular shaped cells with prominent nuclei. This layer of cells lies next to the intima and follows the wave-like folds throughout the fore-intestine. The cell walls are not very distinct, but the basement membrane is quite evident.

Outside of the epithelial layer are found well developed bundles of longitudinal muscle fibers. These are quite evident in all the sections of the fore-intestine but they gradually become smaller in the region of the crop.

Surrounding the longitudinal muscles is a well developed layer of circular muscle. These muscles are numerous in the folds of the oesophageal valve.

The oesophageal valve, (Fig. 4, Plate I), marks the junction of the fore-intestine with the mid-intestine. It consists of six folds which project into the lumen of the stomach. These folds are formed by the projection of the fore-intestine into the mid-intestine, which then fold back upon themselves in an outward direction to the anterior edge of the mid-intestine. At this point the intima of the fore-intestine ends and the digestive epithelium of the stomach begins. The epithelium of the valve is continuous with that of the fore-intestine. Circular muscles are numerous in the folds of the valve and they apparently function in its closing. The circular and longitudinal muscles reverse their positions at the point where the intima ends and the digestive epithelium begins. Strands of peritoneal membrane are evident in sections from this region.

Mid-Intestine.

The mid-intestine or stomach is that part of the alimentary canal posterior to the oesophageal valve and anterior to the pyloric valve.

In this part of the digestive tract there is no cuticular covering of the epithelial cells, and the position of the circular and longitudinal muscle layers is reversed as compared with that in the fore-intestine.

The peritrophic membrane, which is a structureless membrane found in the mid-gut, encloses the food in the stomach thus protecting the delicate secreting cells from injury by sharp food particles. It is apparently secreted near the juncture of the fore-intestine and the mid-intestine, since the sections showing it were from the anterior part of the mid-gut (Fig. 11, Plate II).

The cells of the digestive epithelium vary in size and shape depending upon their physiological condition at the time the insect was killed. In the specimens dissected which had fed very recently or were feeding prior to the time of killing, the epithelial cells are of the columnar type, being long and narrow (Fig. 11, Plate II), and showing holocrine secretion; while the epithelial cells in the specimens which were killed a few hours after feeding are much shorter, indicating that the epithelium had recently secreted. In general the epithelial cells are shorter in the posterior part of the mid-gut, (Fig. 5, Plate I). The nuclei are large and oval in shape, staining deep blue with Delafield's Haemotoxylin.

The secretion of the epithelial cells is holocrine, the entire contents of the cell bursting out into the lumen of the gut, after which the cell is replaced by new cells developed from nidi (nests of embryonic tissue scattered in the base of the epithelium). The nidi (Fig. 11, Plate II) are numerous and lie in the base of the epithelium along the basement membrane. The columnar cells burst as the digestive fluids are needed,

and they are replaced by new cells splitting off on the sides of the nidi, which lengthen and fill with digestive fluid.

The circular muscles of the stomach consist of two narrow layers which are fairly well developed, and are present throughout the length of the mid-gut.

The outer layer of the stomach consists of small strands of longitudinal muscle.

The thin delicate peritoneal membrane is also present.

Hind-Intestine.

The hind-intestine is marked anteriorly by the pyloric valve and posteriorly by the anus.

The pyloric valve (Fig. 5, Plate I) consists of very narrow columnar cells which are arranged in irregular fan-shaped groups. The intima which lines the valve and continues throughout the hind-intestine originates at the junction of the mid- and hind-intestine. These fan-shaped groups of cells probably function as a valve, since this region is surrounded by a heavy layer of circular muscle which upon contraction apparently could close the valve.

The Malpighian tubule attachments have been described under gross anatomy of the alimentary canal. Histological examination of the tubules at their respective points of origin shows that the epithelial cells are very similar to those cells making up the pyloric valve, being narrow and elongate and having conspicuous nuclei. Later they assume the characteristic cuboidal shape a short distance from the point of attachment. Intima is present in the tubules but is difficult to detect a short distance from the point where they join the ileum. In a typical cross-section they are made up of from four to six cuboidal cells with large conspicuous nuclei, and are surrounded by a very thin peritoneal membrane (Fig. 3, Plate I). A cross section from A to B in Fig. 5, Plate I, is shown in Fig. 7, Plate II. This shows the opening through which the excretions from the Malpighian tubules of the first group must pass in entering the ileum.

There is a gradual change from the region of the valve to that of the ileum, the intima becoming more wavy in outline, the epithelial cells and their nuclei becoming larger in size, and the circular muscles decreasing slightly in size. The longitudinal muscles consist of a few isolated strands.

The ileum (Fig. 8, Plate II) forms the connecting link between the pyloric valve and the colon. The layers of intima, epithelium, basement membrane, and circular and longitudinal muscle of the ileum are continuous with those of the colon. In the colon the folds of the intima are less pronounced, and the epithelial cells are slightly larger.

The circular muscles consist of a single layer which is prominent at the anterior part of the colon but gradually decreases in size towards the posterior end.

The longitudinal muscles are fairly well developed at the anterior end and gradually increase in size posteriorly.

The distal ends of the Malpighian tubules also form a layer around the colon. The entrance of the tubules into the delicate nucleated

layer of peritoneal membrane was described under gross anatomy. A cross section of the anterior part of the colon shows the six Malpighian tubules (Fig. 9, Plate II) in the peritoneal membrane.

Proceeding caudad serial sections of the colon show an increasing number of sections of Malpighian tubules. This is due to the convoluted shape of the tubules and the winding course followed by them in the posterior part of the colon. A cross section of the extreme posterior part (Fig. 10, Plate II) shows almost a continuous layer of Malpighian tubules around the colon, which would seem to indicate that the tubules branch.

Woods (1916) states that the Malpighian vessels of *Haltica bimarginata* Say seem to branch irregularly. It was found that they do not branch but follow a very irregular course (Fig. 6, Plate I) in the peritoneal layer. The colon is almost completely covered with tubules near the posterior end, so that in a cross section of this region a number of sections of the same tubule are made, thus forming a continuous layer. The tubules end blindly in the peritoneum at the junction of the colon and rectum.

The rectum connects the colon with the anus. The colon ends rather abruptly and the heavy circular muscle layers mark the beginning of the rectum. The intima and epithelium project into the lumen of the rectum in from five to eight wavy folds, (Fig. 12, Plate II), these becoming more pronounced posteriorly. The nuclei of the epithelial cells are large, the cell walls being indistinct and the cells being somewhat smaller than those of the colon. Outside of the epithelial cells is the basement membrane, which is fairly distinct. The circular muscles are well developed and are composed of three or four layers. Longitudinal muscle is present in a few isolated strands.

SUMMARY.

Morphologically the canal is divided into three primary regions, namely, fore-intestine, mid-intestine, and hind-intestine.

The fore-intestine is represented by the following parts; pharynx, oesophagus, crop, and oesophageal valve.

The mid-intestine is represented by the stomach.

The hind-intestine consists of the following regions; pyloric valve, Malpighian tubules, ileum, colon, and rectum.

Histological examination of the fore-intestine reveals a similarity in structure of the various parts. The layers represented from within out are: intima, epithelium, basement membrane, longitudinal muscle, circular muscle, and peritoneal membrane.

In the mid-intestine the layers from within out are: peritrophic membrane, epithelium, basement membrane, circular muscle, longitudinal muscle, and peritoneal membrane.

The layers in the hind-intestine from within out are: intima, epithelium, basement membrane, circular muscle, longitudinal muscle, and peritoneal membrane.

There are six Malpighian tubules present in *Criocerus asparagi* Linn. The distribution of these tubules is as follows, beginning at their distal ends. From their point of attachment at the distal end of the colon, the tubules follow a convoluted course running cephalad in the peritoneal membrane. They unite at the anterior end of this region to form two common trunks. These two trunks upon leaving the wall of the colon, each split into a single tube and a common stem representing a pair of tubes. The single tubes follow an irregular course in the region of the ileum and finally become attached to an evagination of the epithelium of the pyloric valve. Each common stem soon separates into two tubules which have a long course in the body cavity, running cephalad to the crop. Here they turn caudad following the mid-gut to its posterior end, where the four vessels unite to form a knob-like structure or urinary bladder, which empties into the hind-intestine just posterior to the pyloric valve.

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EXPLANATION OF PLATES.

Plate I.

Fig. 1. Cross-section of oesophagus.
Fig. 2. Cross-section of crop.
Fig. 3. Cross-section of Malpighian tubule.
Fig. 4. Longitudinal section of oesophageal valve.
Fig. 5. Longitudinal section of pyloric valve. This section also shows the posterior part of the stomach, the anterior part of the ileum, and the duct formed by the attachment of the group of four Malpighian tubules.
Fig. 6. Diagrammatic dorsal view showing alimentary canal and Malpighian tubules. The Malpighian tubules on the colon are in the peritoneal membrane.

Plate II.

Fig. 7. Cross-section from A to B in Fig. 5, Plate I, showing the duct of the group of four Malpighian tubules.
Fig. 8. Cross-section of ileum.
Fig. 9. Cross-section of anterior part of colon, showing the six Malpighian tubules in the peritoneal membrane.
Fig. 10. Cross-section of the posterior part of the colon showing a continuous layer of tubules in the peritoneal membrane.
Fig. 11. Cross-section of stomach showing the peritrophic membrane and holocrine secretion.
Fig. 12. Cross-section of rectum.

KEY TO ABBREVIATIONS.

B. M.—Basement membrane.
C. D.—Common duct.
C. M.—Circular muscle.
CR.—Crop.
CO.—Colon.
DU.—Duct.
EPI.—Epithelium.
IL.—Ileum.
INT.—Intima.
L. M.—Longitudinal muscle.
M. I.—Mid-intestine.
M. T.—Malpighian tubule.
M. T. A.—Malpighian tubule attachment.
NI.—Nidus.
OES.—Oesophagus.
OES. V.—Oesophageal valve.
PH.—Pharynx.
PER. M.—Peritrophic membrane.
P. M.—Peritoneal membrane.
P. V.—Pyloric valve.
REC.—Rectum.

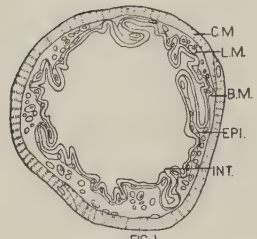


FIG 1.

FIG 3

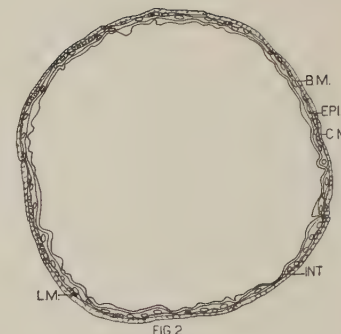


FIG 2

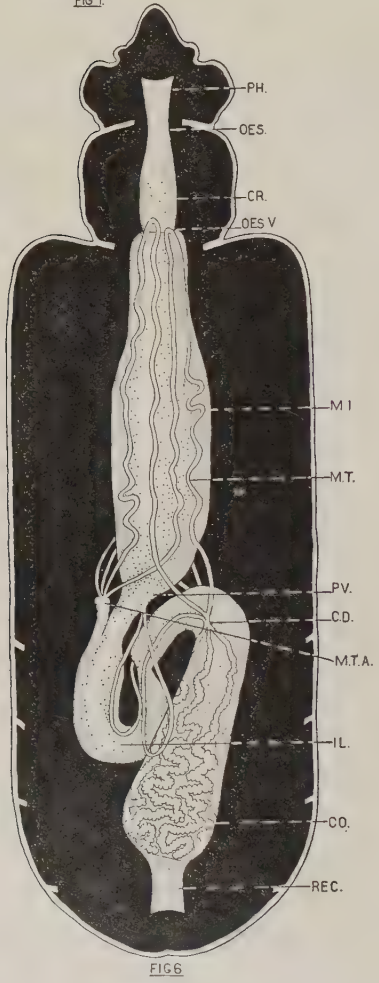
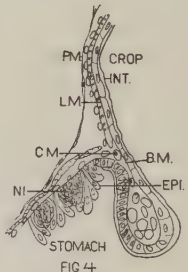


FIG 6



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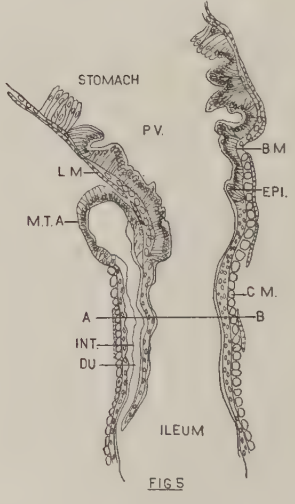

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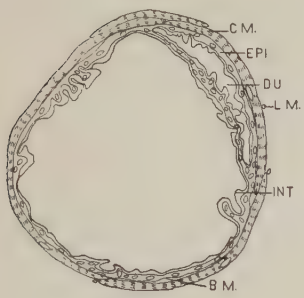
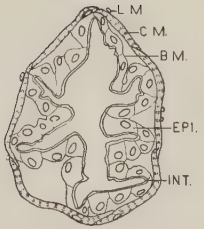


FIG. 7



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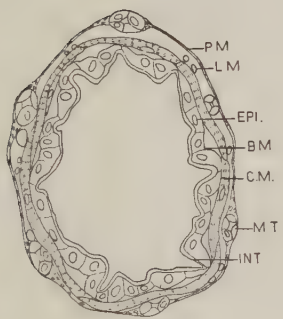

FIG 9

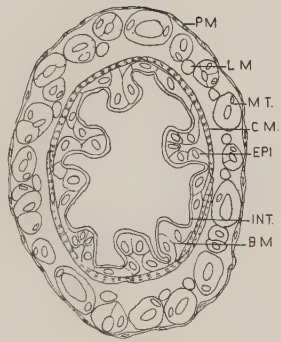

FIG 10

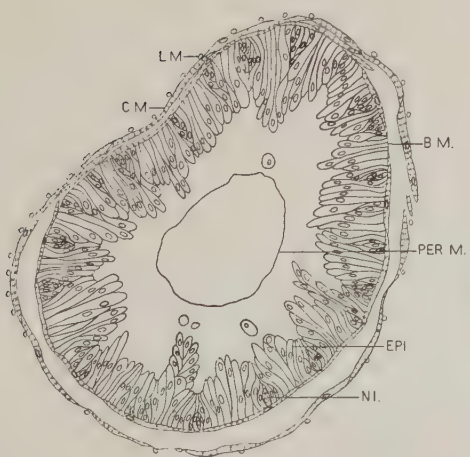

FIG 11.

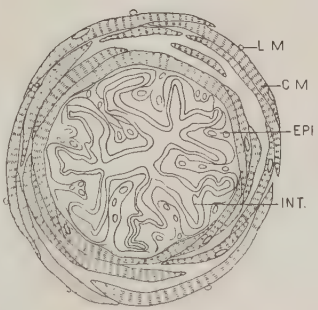

FIG 12

THE ALIMENTARY CANAL OF SPHAERODERUS NITIDICOLLIS CHEV. VAR. SCHAUMI CHD. (COLEOPTERA)*

PAUL EVERETT SCHAEFER.

During the summer of 1930, while collecting insects at the Franz Theodore Stone Laboratory, Put-in-Bay, Ohio, one of the carabidæ was found feeding on snails. The species was identified by Mr. L. L. Buchanan of the U. S. National Museum as *Sphaeroderus nitidicollis Chevrolat variety schaumi Chaudoir*. The species was found in a restricted locality on but one of the islands in that vicinity. The beetle is about two centimeters long, has a narrow head and prothorax, large mandibles and is of a violaceous color. Since the writer is very much interested in Carabidæ in general, at the advice and direction of Dr. C. H. Kennedy a study of the internal morphology of this species was undertaken.

The species ranges from Hudson Bay to northern Virginia but is rarely taken. Comparatively few specimens were found even after intensive search. These were fixed in Kahle's fluid and preserved in seventy per cent alcohol. The study was carried on through the fall and winter, but the scarcity of material made it somewhat restricted. It is hoped that more material may be obtained in order to complete a more intensive study of the morphology and physiology.

The author wishes to express deep appreciation for the suggestions, criticisms and assistance so freely given by Dr. Kennedy and for the helpful comments of many of his fellow-students.

Gross Anatomy of the Digestive Tract.

There are three main divisions of the alimentary canal determined by the embryonic origin. The anterior portion (stomodaeum or fore-gut) arises as an invagination at the cephalic end of the embryo. The posterior portion appears similarly at the caudal end. These two parts, therefore, are ectodermal in origin. The mesenteron or mid-gut is formed by the proliferation of cells in the endodermal tissue and eventually connects the fore-gut to the hind-gut forming a continuous tube.

*Presented in partial fulfillment of the requirements for the degree of Master of Science at Ohio State University.

The three regions are further differentiated to forms:

1. Fore-gut.
   a. Mouth or buccal cavity.
   b. Pharynx.
   c. Oesophagus.
   d. Gizzard (proventiculus).
   e. Oesophageal valve.
2. Mid-gut (venticulus).
   a. Anterior mid-gut.
   b. Posterior mid-gut.
3. Hind-gut.
   a. Pyloric valve.
   b. Malpighian tubules.
   c. Ileum.
   d. Rectum.
   e. Anal opening.

Though some variation occurs the different parts will usually be found to lie as follows: The fore-gut passes caudad along the median axis to the first abdominal segment where it joins the mid-intestine. The mid-intestine continues caudad for about a quarter of its length bending to the right in the second abdominal segment then sharply to the left. The posterior quarter of the mid-gut curves dorsad, at right angles to the antero-posterior axis, and joins the ileum at about the fourth abdominal segment. The ileum curves left and ventrad sometimes forming a sharp half loop, to the sixth abdominal segment joining the rectum, which is more or less covered by the chitinous sheath surrounding the genitalia. The rectum is bellows-like and capable of considerable elongation.

The Fore-Intestine.

The alimentary tract of the adult is about three cm. long, approximately one and a half times the length of the body, of this, the fore-gut comprises a little more than one fourth. The *pharynx* appears as a short dilated portion just posterior to the mouth. The *oesophagus* normally is smaller than the pharynx but is capable of some dilation. The *gizzard* or proventriculus may be distinguished as an enlarged rounded portion just anterior to the junction of the fore-gut and the mid-gut. The *oesophageal valve* is not apparent externally.

The Mid-Intestine.

The mid-intestine forms somewhat more than a third of the entire tract and is divided into two distinct portions approximately equal in length. The anterior portion is about twice the diameter of the posterior part but both are densely covered with papillæ those on the posterior portion being smaller, gradually diminishing in size towards the distal end.

The Hind-Intestine.

The beginning of the hind-gut is marked by the *malpighian tubules* of which there are four each having a separate entry, though the two dorsal tubes are somewhat nearer each other than the dorso-ventral

tubes on either side. (See Fig. 12, Plate III). The tubes are long and greatly coiled, so much so that they could not be measured in the preserved material, no fresh material being available. The *pyloric valve* is immediately anterior to the tubules but is not distinguishable externally. The hind-gut makes up approximately one-third of the digestive tract. The *ileum* is but little more than half the diameter of the posterior mid-gut though it comprises a little less than two-thirds of the hind-intestine. There appears to be a constriction at the junction of the ileum and rectum but no valve was demonstrated. The *rectum* is somewhat cone-shaped the anterior portion being the larger, in this region the ovoid rectal pads, six in number, show plainly through the transparent wall. Due to the bellows-like form of the rectum it may be elongated considerably.

On either side of the rectum appears a comparatively large ovoid sac the ducts of which open one on either side of the anus. These are probably the anal glands from which a rather acrid fluid is emitted if the insect is disturbed.

Histological Structure of the Alimentary Canal.

Histological Structure of the Fore-Intestine.

The fore-intestine being formed by the invagination of the body wall has approximately the same structure. Microscopical study of cross-sections from this region demonstrates the following differentiated areas: (1) a chitinous inner lining, intima, (2) an epithelium of hypodermal cells, (3) longitudinal muscles, (4) circular muscles, (5) and an enveloping membrane of connective tissue, "Peritoneum." (This term is improperly applied to insect tissue.)

The general structure of the fore-gut is the same throughout though some differences in detail may be noted.

The chitinous intima is plainly visible from the mouth to the junction of the fore-intestine and the ventriculus. In the anterior portion of the tube it is smooth and comparatively thin, but posteriorly it becomes thickened and densely covered with cilia-like structures, within the gizzard chitinous pads are found between the teeth. (See Fig. 5, Plate II.)

The epithelial layer of hypodermal cells is not so apparent in the oesophagus, individual cells being somewhat flattened. In the gizzard, however, they are either cuboidal or columnar in form and may be readily distinguished. (See Fig. 5, Plate II).

The longitudinal muscles of this region are gathered into four groups which lies in folds of the epithelium. Cephalad these groups are small, becoming larger in the pro-ventriculus, (See Figs. 2 and 4, Plate I, Fig. 5, Plate II).

The circular muscles appear outside the longitudinal muscles in scattered strands near the head but increasing to several layers around the pro-ventriculus (gizzard). (See Figs. 2 and 4, Plate I, Fig. 5, Plate II).

Traces of a "peritoneal membrane" composed of connective tissue may be found here and there, though it is largely obscured by the fatty tissue surrounding the fore-gut.

The oesophageal valve is located at the junction of the fore- and mid-intestine. This consists of a fold of the fore-gut which extends but slightly into the lumen of the mid-gut. At this point the numerous circular muscles largely fill the constriction between the gizzard and the ventriculus. In this region there is a complete reversal in the position of the muscles, the longitudinal muscles of the mid-gut lying outside the circular muscles. (See Fig. 3, Plate I).

Histological Structure of the Mid-Intestine.

The mid-intestine which is bounded anteriorly by the oesophageal valve, posteriorly by the pyloric valve, is divided into two distinct regions approximately equal in length, the anterior portion being nearly twice the diameter of the posterior part. This region is entirely covered by papillæ, those of the fore part being much larger than the ones on the hinder portion.

A histological study of the mid-gut shows the two parts to be much the same save for size. Four rather definite layers are distinguishable: (1) epithelium of endodermal tissue, (2) circular muscles, (3) longitudinal muscles and (4) connective tissue termed the "peritoneal membrane."

The epithelial layer may vary in form and appearance depending on whether it is in the resting phase or the secretory phase. Shortly after taking food the cells are distended some of them breaking off to supply digestive fluids (holocrine secretion). These cells burst and pass off, new cells being formed by certain regenerative tissues contained in the crypts. (See Fig. 8, Plate II). There is some evidence for a merocrine secretion as well, for large globules of liquid may be noted exuding from the crypts during certain phases of the digestive process. (See Fig. 8, Plate II).

The papillæ which cover the surface of the mid-intestine, commonly termed crypts, contain at the tip a mass of generative tissue called a nidus. These nidi probably form the secretory cells of the epithelial layer. The nidi have sunken into the wall of the ventriculus, eventually breaking through to form the crypts which appear on the outer surface of the mid-gut. These are not what are ordinarily termed gastric coecae.

Just outside the basement membrane the circular muscle may be seen; ordinarily two or three layers appear.

The longitudinal muscles (which are reversed in position relative to those of the fore- and hind-gut) appear only in scattered groups and are not numerous.

A very thin "peritoneum" surrounds the entire mid-intestine. (See Figs. 6 and 7, Plate II).

(Although a differentiation occurs in the two regions of the mid-gut no valve was found between them and no division in function is discernible unless the fore part which has the larger crypts is primarily digestive and the hinder portion absorptive. However, much the same type of epithelial cells appear in both regions. (See Figs. 6 and 7, Plate II).

Histological Structure of the Hind-Intestine.

Externally the division between the hind-intestine and the ventriculus is marked by the malpighian tubules. Those are made up of large irregular cells with rather large ovoid nuclei. (See Fig. 21, Plate III). The cells may vary in number from five to twelve in cross section. The inner surface of the tubules appears to be striated, though this does not appear for a short space from the opening into the lumen of the gut. The outer surface is covered by a very thin membrane.

A histological examination of the hind-gut reveals, (1) an intima, (2) an epithelial layer of hypodermal cells, (3) a layer of circular muscle, (4) an outer layer of longitudinal muscle and (5) a "peritoneum" of connective tissue.

Internally the division between the ventriculus and the hind-intestine is marked by the pyloric valve. This consists of a definite fold in the epithelial layer of the ileum. (See Fig. 9, Plate III).

The intima in the region of the pyloric valve is so thin that it is not apparent though it may be plainly seen in the rectum.

The inner layer of longitudinal muscle which ordinarily should be found in the hind-gut does not appear.

The circular muscles which function in closing the valve are very numerous. (See Fig. 9, Plate III).

Just outside the layer of circular muscle may be found a few strands of outer longitudinal muscle. (See Fig. 9, Plate III).

A very thin "peritoneum" is found surrounding the pyloric region.

The intima of the ileum is so thin it appears merely as a line, but the epithelial layer is very thick. The epithelial cells in the ileum are columnar and form folds which almost completely fill the lumen of the tube. Two or three layers of circular muscles are visible but the longitudinal muscles are evident only as a few scattered groups.

The rectum is much greater in diameter than the ileum, though the walls are very thin, so thin that in the anterior portion the six large ovoid rectal pads lying on the inner surface may be plainly distinguished. The intima of the rectum is thicker than in any other part of the hind-gut.

The rectal pads are composed of large columnar cells which form pads between the intima and the basement membrane. (See Fig. 14, Plate III). Outside the pads the thin epithelial layer is visible.

The circular muscles are but scattered strands and the longitudinal muscles may be seen only in one or two isolated groups.

The connective tissue or "peritoneum" appears only here and there. (See Fig. 14, Plate III).

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EXPLANATION OF PLATES.

Plate I.

Fig. 1. Dorsal view showing gross dissection of the Alimentary Canal. OES.—oesophagus; GIZ.—gizzard (proventriculus); A.M-GUT—anterior mid-gut; P. M-GUT—posterior mid-gut; M. TUB.—malpighian tubule; IL.—ileum; REC. PAD—rectal pad; AN. GL.—anal gland.

Fig. 2. Cross-section through the Oesophagus. EPI.—hypodermal epithelium; LU.—lumen of fore-intestine; IN.—intima; C. MUS.—circular muscle; L.MUS.—longitudinal muscle; MUS.?—probably muscle. (This section is magnified approximately one and a half times more than the section of the oesophagus caudad to this in Fig. 4.)

Fig. 3. Longitudinal section showing the Oesophageal Valve. EPIT.—endodermal epithelium; OES. VL.—oesophageal valve; LU.—lumen of fore-intestine; EPI.—hypodermal epithelium; IN.—intima; OES.—oesophagus; CE.—crypt on mid-gut; C. MUS.—circular muscle; C. TIS.—connective tissue, "Peritoneum;" L. MUS.—longitudinal muscle.

Fig. 4. Cross-section through the Oesophagus posterior to Fig. 2. C. MUS.—circular muscle; C. TIS.—connective tissue, "peritoneum;" L. MUS.—longitudinal muscle; LU.—lumen of fore-gut; IN.—intima; EPI.—hypodermal epithelium.

Plate II.

Fig. 5. Cross-section through the Gizzard (proventriculus). C. TIS.—connective tissue, "peritoneum;" C. MUS.—circular muscle; L. MUS.—longitudinal muscle; EPI.—hypodermal epithelium; IN.—intima; LU.—lumen of fore-gut.

Fig. 6. Cross-section through the anterior Mid-Gut. LU.—lumen of mid-gut; EPIT.—endodermal epithelium; C. MUS.—circular muscle; L. MUS.—longitudinal muscle; CR.—crypt.

Fig. 7. Cross-section through the posterior Mid-Gut. LU.—lumen of mid-gut; EPIT.—endodermal epithelium; C. MUS.—circular muscle; L. MUS.—longitudinal muscle; CR.—crypt.

Fig. 8. Longitudinal section through a Crypt of the anterior mid-gut. HOL.—holocrine secretion; EPIT.—endodermal epithelium; C. MUS.—circular muscle; L. MUS.—longitudinal muscle; C. TIS.—connective tissue, "peritoneum;" SEC.—globule of secretion (merocrine).

Plate III.

Fig. 9. Longitudinal-section through the Pyloric Valve. EPIT.—endodermal epithelium; C. MUS.—circular muscle; L. MUS.—longitudinal muscle; PY. VL.—pyloric valve; C. TIS.—connective tissue, "peritoneum;" LU.—lumen of hind-intestine.

Fig. 10. Detail drawing of Fig. 12. M. TUB.—malpighian tubule; C. TIS.—connective tissue, "peritoneum;" L. MUS.—longitudinal muscle; CR.—crypt; C. MUS.—circular muscle; EPI.—hypodermal epithelium (?); ?—probably epithelial tissue; LU.—lumen of hind-gut.

Fig. 11. Cross-section through a Malpighian Tubule. S. B.—striated border; LU.—lumen of tubule; C. TIS.—connective tissue, "peritoneum."

Fig. 12. Diagrammatic drawing made from series of sections to show entry of each of the four Malpighian Tubes.

Fig. 13. Cross-section through the Ileum. L. MUS.—longitudinal muscle; C. MUS.—circular muscle; LU.—lumen of hind-gut; EPI.—hypodermal epithelium; C. TIS.—connective tissue, "peritoneum."

Fig. 14. Cross-section through the Rectum showing the Rectal Pads. REC. PAD—rectal pad or gland; IN.—intima; EPI.—hypodermal epithelial tissue; L. MUS.—longitudinal muscle; C. MUS.—circular muscle; LU.—lumen of hind-gut.

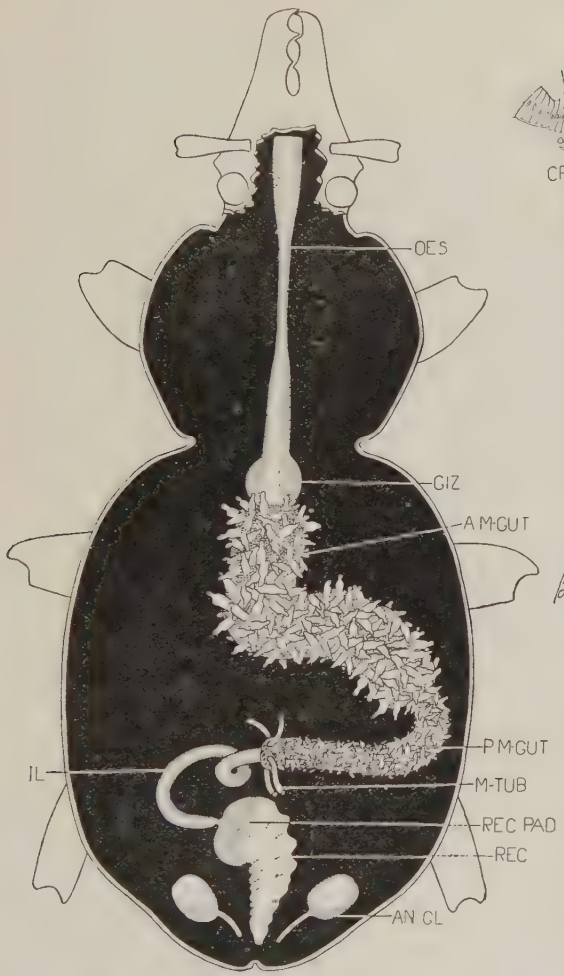
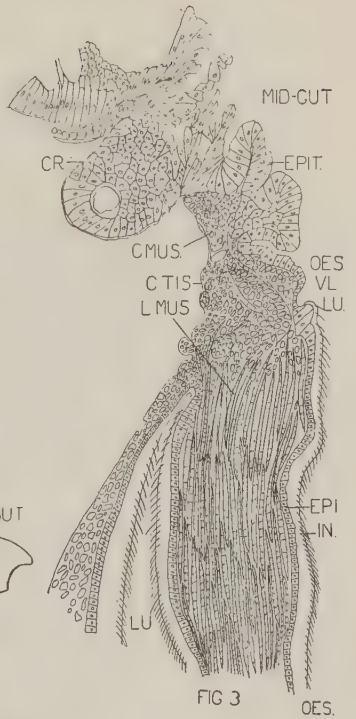


FIG 1



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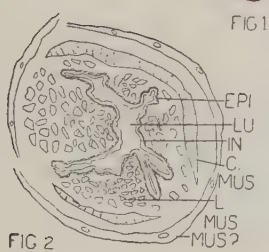

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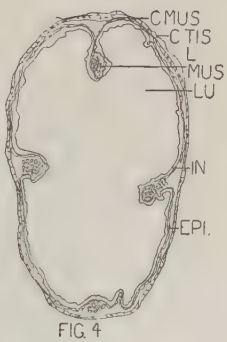

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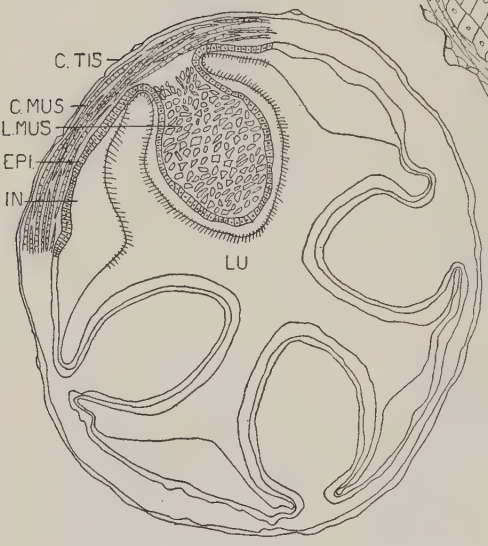

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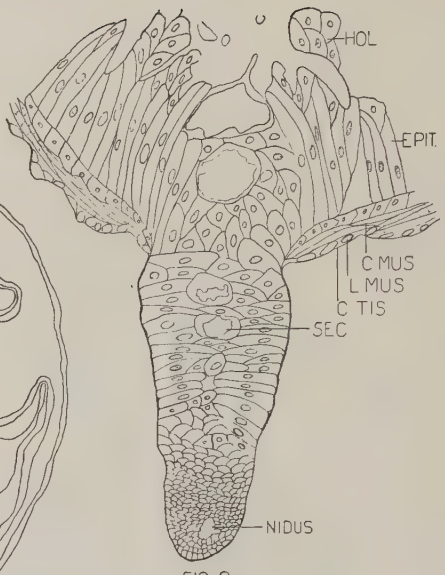

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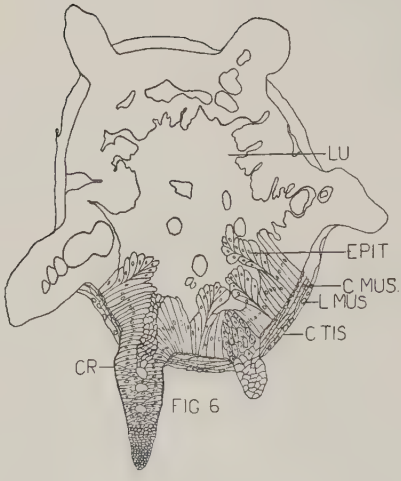

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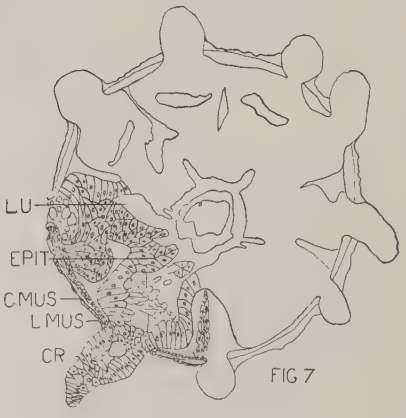

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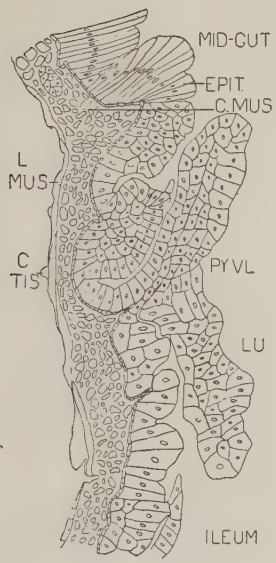

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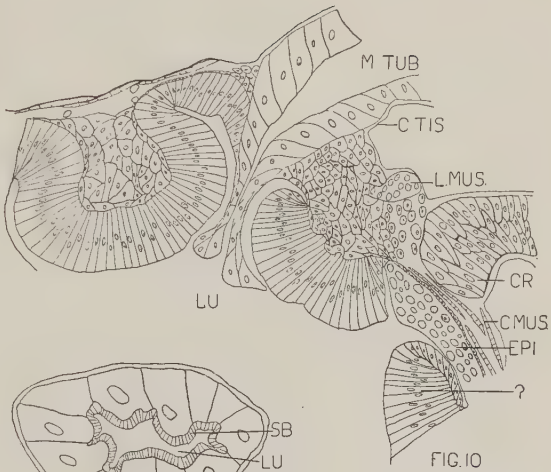

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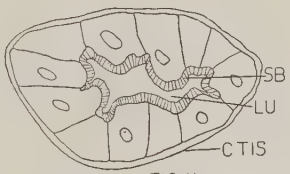

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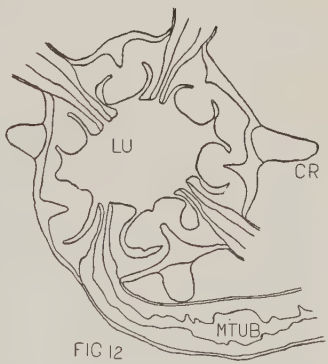

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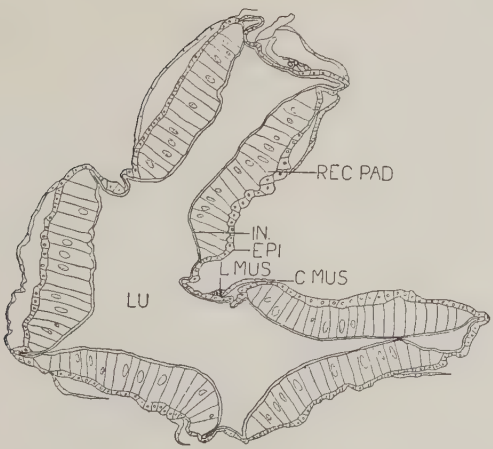

FIG 14

FIG 13

BISPORANGIATE INFLORESCENCES IN PSEUDOTSUGA.

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In June, 1926, while examining some Douglas fir trees, (*Pseudotsuga taxifolia*, Britton) about fifteen years of age, on the grounds back of the State Capitol at Albany, N. Y., the writer noted, on one, some inflorescences which, although growing in normal position among other pistillate flowers, had an abnormal appearance. Specimens were accordingly collected and examined more closely with regard to the arrangement and structure of the various parts.

The strobili in question bore normal, ovulate scales, with bracts, on the upper portion, and staminate structures on the lower half of the axis. They were not so well developed as the normal pistillate flowers found on the same and neighboring trees, the largest measuring only 25 mm. in length, of which the lower 10 mm. were occupied by the stamens.

The sporophylls, both macro- and micro-, at the upper and lower extremities respectively, of the axis, appeared entirely normal in size and structure. Along the mid-section of the axis, however, sporophylls were found which apparently constituted transitional structures. In some cases there were normally shaped ovuliferous scales which, however, bore ovules that were distorted and apparently abortive; in others, the entire sporophyll was abnormal, with a scale-like structure at the base, surmounted by a poorly developed stamen, with an elongated spur.

During the past few years, as time permitted, the writer has examined the literature on this subject, without finding any previously recorded observation of this kind relative to *Pseudotsuga*. Similar occurrences in the case of a number of other conifers, however, have been reported. Dickson (1) described such inflorescences for *Picea Abies*. Bisporangiate cones on *Sequoia* were reported by Shaw (2). Fisher (3) observed abnormal cones on *Pinus laricio* which, though in the normal position of the staminate flower, had staminate structures only on the lower four-fifths of the axis, with pistillate

on the remainder. Kirkwood's (4) description of bisporangiate flowers on *Larix occidentalis* is almost parallel to the condition described in this paper on *Pseudotsuga* except that in the former, the abnormal cones were as large as the normal ovuliferous ones. Dallimore and Jackson (5) mention the occurrence of bisexual cones in the case of *Pinus thunbergii*, though not giving a specific authority for the observation.

The writers cited above agree for the most part in their interpretation of the phenomenon of bisexuality in conifers, namely, as exemplifying the homology of the stamen with the bract of the carpellate cone. Kirkwood cites Coulter and Chamberlain's well-known work on "The Morphology of Gymnosperms" in this regard. Fisher (loc. cit.) goes further and takes up the discussion relative to the homology of the ovuliferous scale. In this he favors the theory that the scale is a secondary structure developed as a ligulate or chalazal outgrowth of the carpellate bract, citing a previous paper by Bessey in support of this attitude.

More recently, Schaffner (6) has discussed in considerable detail the matter of sexual reversal in monoecious inflorescences. Although this writer does not touch directly upon conifers, the paper cited has some bearing on the principles involved in the occasional development of bisexual cones in the Coniferæ and is of still further interest by reason of a description which is given of a bisexual catkin of *Salix amygdaloides*. Although this was considered as being essentially a staminate catkin, the arrangement of the organs was the same as found in similar inflorescences among the conifers, the pistillate appearing on the upper and the staminate on the lower part of the axis with various transitional structures between. A more complete description of the finding of this and other sexual phenomena in *Salix* is given by the same author in a previous paper (7).

(1) Trans. Edin. Bot. Soc. 6: 418–422, 1860.
(2) Bot. Gaz. 21: 332–339, 1896.
(3) Ohio Nat. 6: 396–397, 1905.
(4) Bot. Gaz. 61: 256–257, 1916.
(5) Handbook of Coniferæ: 466, London, 1923.
(6) Ohio Jour. Sci. 21: 185–200, 1921.
(7) Ohio Jour. Sci. 19: 409–416, 1919.

ABSTRACTS.*

PSYCHOLOGY SECTION.

Suggestibility as Influenced by the Form of the Question.—By HAROLD E. BURTT, Ohio State University.

Moving picture news reels were presented and subjects questioned immediately. Six forms of question were used over 5000 times each as follows:

(a) Did you see a.....; (b) Did you see the.....; (c) Didn't you see a.....; (d) Didn't you see the.....; (w) Was there a.....; (x) Wasn't there a.....

The erroneous admission of the presence of an object was construed to reflect suggestibility in the form of the question. Three aspects were analyzed, the nature of the article, the negative vs. positive form, and the subjective vs. objective form. Results regarding the first of these were equivocal. There is a somewhat statistically significant trend for the negative to carry greater suggestion than the positive form although there seems one clear exception to this trend. With regard to the subjective and objective forms the latter shows clearly a higher degree of suggestibility.

An Experiment on the Relative Effectiveness of the Lecture-quiz and the Recitation Methods of Class Instruction in Elmentary Psychology.—By H. H. REMMERS, Purdue University.

The object of this experiment was to determine the relative achievement of students under two different methods of instruction in Elementary Psychology: the lecture-quiz method and the recitation method. The lecture-quiz group containing approximately 150 students met twice a week for lecture and once a week in groups of 35 to 40 for discussion and quiz. Ninety-seven students in the lecture-quiz group were matched with 97 students in other classes meeting three times a week in groups of 35 to 40 on the basis of 4 criteria—sex, school of enrollment in the University, and the average percentile score on the Iowa Chemistry Aptitude Test, Iowa Mathematics Training Test, Purdue University English Placement Test, and National Council Psychological Examination. Achievement was measured in terms of objectively scored tests, daily written work, and an essay type of examination. Students' attitudes toward instructors and the method of instruction were also obtained. The major finding of the experiment is that the larger group under the lecture-quiz method did slightly

*The Abstracts for the Section of Psychology were not received by the Secretary until the July number of the Journal containing the Proceedings of the Academy had been printed and was nearly ready for mailing.

but not statistically significantly better on the average than did the smaller recitation classes—this notwithstanding the fact that student attitude rather emphatically favored the less formal recitation method.

The Anticipation of Correct Responses as a Source of Error in Learning Serial Responses.—By Frederick Hillis Lumley, Ohio State University.

Forty subjects learned three maze patterns on a typewriter multiple choice maze. These maze patterns consisted of two series of twenty letters and one series of forty letters. Analysis of the types of errors showed that the subject anticipated responses which would have been correct further on in the series. The frequency of the anticipation errors was inversely proportional to the degree of anticipation. Thus responses, which would be correct in the near future, were anticipated more often than responses which would be correct in the distant future. As learning progressed the ratio of the near anticipations to the far anticipations increased. Analysis of the published data of other investigators shows this factor of anticipation.

The Effect of Emotional Stimuli on the Activity Level of the White Rat.—By James R. Patrick.

Two groups of fed rats, one rat at a time from each group, were put into an "activity maze" for a period of two minutes each. One group of ten rats constituted the control. The second group (10 rats) was the experimental group. The activity of the control group was recorded under normal conditions. But the experimental group was subjected to emotional stimuli during the full two minute period they were in the maze. The results show that spontaneous overt activity, under the present conditions, is inhibited when rats are not operating under a drive but are confronted with emotional stimuli as is afforded by the sounding of buzzers. The control group, without the influence of emotional stimuli, showed 27 per cent increase in activity over the experimental group. Results from experiments reported in the literature seem to show that when the rat is operating under a drive, as in a learning situation, and when he encounters emotional stimuli that excess amount of behavior is shown. The present research, along with the others reported, indicates that the behavior level of the white rat is influenced by both "internal" and "incidental external" sources of stimulation while the rat is in the maze.

A Comparison of the High Relief Finger Maze and An Improved Form of the Stylus Maze.—By T. C. Scott and B. B. Nelson, Ohio University.

The object of this investigation was to make a comparison between the high-relief finger maze and an improved form of a stylus maze. This stylus maze was so constructed that retracing was prevented. The stylus was also of such a nature that it fit snugly and the subject could not wander around in the groove or have the feeling of being lost.

One hundred subjects learned a stylus and a wire maze of identical pattern and size. Group 1 of 50 subjects learned the stylus maze the

first day and the wire maze the second day. Group 2 of 50 subjects learned the wire maze the first day and the groove maze the second day. In both cases the subjects were not told that the patterns were the same. Group 1 required a few more trials and errors, but less actual running time, to learn the stylus maze the first day than Group 2 did to learn the wire maze. These differences, however, were highly unreliable, particularly in the case of trials and errors, the obtained difference between the means being less than the standard error of difference. The results the second day offered further evidence of this unreliability. About the same number from each group recognized the pattern the second day.

The relative difficulty of the respective alleys of the two mazes indicates that they are measuring the learning function in the same way. The correlation computed in terms of the total number of errors made on the respective alleys in the two mazes is .976.

The reliability coefficients were computed for the two mazes in terms of errors on the first ten trials and show the stylus maze to be somewhat superior to the finger maze for learning experiments.

Twenty-four subjects in each group of 50 were boys, giving sex groups of 48 boys and 52 girls. These two groups offer differences in favor of the boys which are more reliable than those existing between the two maze groups.

An Objective Study of Student and Faculty Attitudes Toward Academic Honesty.[1]—By C. O. Mathews, Ohio Wesleyan University.

It was the purpose of this study to discover the nature and variations of attitudes toward academic honesty among students and faculty members of a certain institution where an honor system had been functioning for about twenty-five years. As a means of tapping attitudes an objective blank containing thirty-six descriptions of honesty situations and one item concerning the reporting of observed dishonesty was constructed.

Responses from 494 representative college students show that there is an extremely wide variation in respect to the kinds of academic conduct that they can justify. There was not one situation of the thirty-six but that was justified by at least four per cent of these students. Only one item was unanimously agreed upon by the faculty.

The juniors and seniors ranked below the freshmen and sophomores in respect to their sense of academic honesty. Women exceeded men in all classes in this respect. There was a very wide gap between the opinions of the students and faculty. Both seemed to be more lenient in their attitude toward dishonesty in preparing assignments than in taking examinations.

In respect to reporting observed dishonesty only one-third of the students and two-thirds of the faculty justified it. Women were more favorable to reporting than men; seniors less favorable to it than the

[1]This is a portion of a faculty report on the honor system at Ohio Wesleyan University. The members of the committee were Professors Diem, Lewis, Manchester, Murray and Mathews (chairman).

other classes; and those with the most favorable attitudes toward honesty were most favorable to reporting dishonesty.

When honest opinions vary as widely as the ones expressed by these persons, and when rationalizations to justify most any action are so easy to construct, is it any wonder that honor systems seem ineffective and that the problem of academic honesty is always at hand?

Rating Scales in Industry.—By RICHARD STEPHEN UHRBROCK, Industrial Relations Division, The Procter and Gamble Company, Cincinnati, Ohio.

Four types of rating scales are most widely used in validating psychological and educational tests in industrial situations.

1. *Order of Merit:* Lists of names of persons to be rated are prepared and presented to judges. The judges are asked to rank the men from best to poorest, and to indicate their ratings by numbering the names.
2. *Man-to-Man:* Traits are defined. A master rating scale is prepared by each judge, who lists the names of persons known to him who possess, in varying degrees, the qualities to be rated. New men are compared with the well-known individuals whose names appear on the master scale. Numerical values are assigned to points on the scale.
3. *Graphic Rating Scale:* Traits considered essential for success on a given job are defined. Degrees of the traits are indicated by means of descriptive phrases. Judges are asked to check the items that most clearly describe the behavior, or attributes, of the man being rated. Each step on the scale is given a numerical value.
4. *Paired Comparison:* The name of each man to be rated is paired with the name of every other man in the group under consideration. Judges are asked to check the name of the better man in each pair.

With ratings upon each man in a group, obtained by means of one or more methods, it becomes possible to rank the members of the entire group under consideration, and to isolate the best third, and the poorest third, for detailed study.

Scientists and Church Membership.—By HARVEY C. LEHMAN AND PAUL A. WITTY, Ohio University and Northwestern University.

In this paper tables are presented which set forth the percentages of individuals from several branches who stated their church affiliations when writing their autobiographical sketches for *Who's Who in America*. Some interesting age differences are presented also.

The names of the most outstanding scientists in the United States were obtained from the 1927 edition of *American Men of Science*, the biographical directory edited by Cattell. Data regarding church membership were obtained from the 1926–1927 edition of *Who's Who in America*.

It is possible that these data indicate also the relative seriousness with which various types of scientists take their church membership. If the latter conclusion be valid it is clear that the physicists consider church membership most seriously; the physiologists, the psychologists, and the anatomists, less seriously, and that older scientists look upon religious denominations less seriously than do younger ones.

The more plausible explanations (from the authors' points of view) are also presented.

The Mental Status of Reformatory Women.—By C. H. Growdon, Ohio Bureau of Juvenile Research.

This study reports the results of a mental survey covering a five-year period beginning July 1st, 1925. The total number of prisoners examined during this time was 2185, of whom 70 were discarded because of unsurmountable language difficulties. Of the number examined 1312 were white adult women, of whom 432 were felons, and 880 misdemeanants. The negro population was 803, of whom 226 were felons, and 577 were misdemeanants.

The method of examination was that of group tests of three varieties, namely, general intelligence tests (Army Alpha, or Morgan's Mental Test), performance tests (Pintner Non-language Tests) and literacy tests (Ohio Literacy). These were supplemented by interviews and individual tests whenever there was good reason to doubt the accuracy of the ratings obtained by group examination. After each prisoner had been given the battery of three group tests the mental ages thus obtained were combined into a single mental age rating by a process of weighting which gave the general intelligence test a weight of two points, the literacy and performance tests a weight of one each in a scale of four.

The mental ages of the prisoners were then grouped together into frequency tables showing the distribution according to race, and crime committed. These distributions were then compared with the mental age norms established for the general population of each race by the army psychologists during the World War. (There are no comprehensive mental age norms for the general female population. We assume that they would parallel those for men had they been established.)

In addition to the comparison on the basis of mental age distributions a more direct estimate of the relationship between imprisonment and mental level was obtained by calculating a "prison ratio" for each mental age, and for each variety of crime. This ratio is obtained by dividing the percent of frequency of any given mental age as found in the population at large, by the percent of frequency found among prisoners at the same mental age. The results are presented in a series of tables and curves.

The main conclusions reached are as follows:

1. On the basis of median mental ages, white female prisoners rated approximately 2.0 years lower than the general white population. White felons gave a median mental age of 11.26 years, white misdemeanants gave a median of 10.02 years.

2. On the same basis negro prisoners rated 1.45 years lower than the general negro population. Negro felons gave a median mental age of 8.65 years, negro misdemeanants gave exactly the same median.

3. On the basis of smoothed percentile curves, the median mental ages rate the prisoners convicted of various crimes thus in decreasing order of mentality:

White prisoners: Forgery and embezzlement, grand larceny, petit larceny, murder, burglary, sex offenses other than prostitution, robbery, prostitution, contributing to delinquency and dependency, violation of the liquor laws, and various types of assault.

Negro prisoners: Forgery and embezzlement, petit larceny, prostitution, grand larceny, contributing to delinquency and dependency, murder, violation

of the liquor laws, various types of assault, robbery, sex offenses other than prostitution, and burglary.

4. The prison ratios show that, for both races, the mental ages from six to ten years send in a relatively high excess of prisoners, that fewer than the expected number come from the mental levels of eleven to fourteen years, and that at fifteen and sixteen years there is a tendency to increase beyond the ratios set by the mental ages of eleven to fourteen. In the case of white prisoners below the mental age of ten years the prison ratios vary from 1.76 to 9.00 times as many in prison as in the general population. In the case of negroes the prison ratios at these same ages seldom exceed 1.5 times the rate in the general negro population.

5. On the basis of prison ratios it appears that mentality is a much greater factor in the conviction of white female delinquents than in the case of negroes, and that persons of average intelligence are less liable to conviction than those higher or lower than average.

Some Recent Findings in the Part and Whole Methods of Learning.—By C. C. Wood.

The investigation from which the following report is taken was prompted by the old quarrel which started more than thirty years ago and which still rages. Steffen, Pyle, Snyder, Freeman, Dolan, Pechstein, Reed, Brown and others have all made substantial contributions.

Most of the investigators named above have found the whole method superior to the pure part method or to any of the modified part methods. Pechstein and Reed are two of the outstanding supporters of the part method of learning. In the light of these investigations the writer set out about three years ago to satisfy, as far as possible, his desire for first hand information concerning this matter of learning.

Ten University students, five men of graduate rank and five undergraduate women, served as subjects. The material for learning consisted of fifteen series of nonsense syllables, twenty-four syllables to the series.

Five methods were used, the pure part, the whole, the progressive part, the direct repetitive and the reverse repetitive. The methods were so rotated that the effects of practice were duly equated, taking care of the transfer effect of each subject's first learning upon the following series.

THE EFFECTS OF PRACTICE ON THE RELATIVE EFFICIENCY OF WHOLE AND PART METHODS.

Our primary interest just now is in the effects of practice on the relative efficiency of the various methods.

There are several problems involved in the general effects of practice. They are (1) Individual differences (2) the effects of choice of criterion (3) the factors conditioning improvement. We wish to answer three questions which may be stated here; they are:

(1) Does practice accentuate or minimize the difference of methods?

(2) What are the relative amounts of change in the efficiency of the various methods?

(3) To what extent is there correlation between the values of the methods?

In answer to the first question our data indicates that practice minimizes differences, in many instances bringing them almost to the vanishing point. For example the difference in trials between the

best and poorest methods, in group I, decreased, from the first to third round, 60.5 per cent, for group II, the decrease was 17.6 per cent between the first and second rounds.

In errors, these decrease in differences were respectively, 65.8 per cent and 34 per cent.

In time, these decreases in differences were, respectively, 91 per cent and 30 per cent.

In answer to the second question our data shows that in every instance the method that was least effective in the beginning showed the greatest improvement and in every instance save one, the method that was most effective in the beginning showed the least improvement.

In the matter of question three, our data shows that correlation became less perfect as practice proceeded.

After the first round, the three criteria give results which were decidedly out of agreement.

Measured by all criteria the effectiveness of the methods ranks as follows:

1. Direct Repetitive.
2. Progressive part.
3. Reversed Repetitive.
4. Pure part.
5. Whole.

In finality the writer wishes to say that the limits of improvement were not reached for any method in this investigation.

How long improvement can continue or just what the limits of improvability are, is a matter of individual capacity. Until the limit of efficiency is reached, improvement is possible. The writer believes that the feeling of necessity has goaded the subjects into a more intensive effort to excel by the whole method procedure than by the part methods. It is therefore possible that the whole method is as near or nearer the limit of efficiency as any of the part methods.

Collection of "Progress" Indices for Ohio Counties.—By C. W. Hall.

In an effort to obtain a measure of the economic, social, educational and health status of each Ohio county, data concerning 157 variables have been collected. These data have been converted into indices. A few of these indices are: percentage of farms located on hard surface roads, tuberculosis death rate, birth rate, percentage of homes having telephones, per capita wealth, per capita sale of Red Cross stamps, average intelligence of high school seniors and the average experience of teachers. From this large group of indices, the best indices for predicting school success will be selected. The variables thus selected will be combined into an index which will be used to secure a socio-economic rating for each Ohio county.

The paper points out many difficulties encountered in using the statistics collected by the several state departments. The most serious errors are introduced by (1) the arbitrary determination of community limits in terms of political units (2) the impossibility of using the same units for all variables (3) the registration in one community of statistics that actually pertain to another community, and (4) the lack of adequate checks. These difficulties seriously impair the usefulness of much of the data gathered by the state. It is suggested

that this situation could be remedied, at least in part, by the appointment of a state director of statistics charged with the improving of techniques and coordinating the work of various state statistical divisions.

The Effect of Hypnosis on Long Delayed Recall.—By JOHN M. STALNAKER, Purdue University.

Twelve subjects in recalling 92 selections of prose or poetry learned a year or more before, were able to reproduce on the average 67 per cent more in the trance than in the waking state. A practice effect of 14 per cent increase of the second condition over the first was found, although a counterbalanced order prevented this from influencing the final results. The subjects were found to improvise the poetry where their literal memory proved inadequate, to a greater extent in the trance state.

The Effect of Rhythm and Reverie on the Machine Worker.—By STANLEY B. MATHEWSON.

This paper discusses what the machine is doing for the human—doing for him emotionally, not economically.

Machine workers whose jobs permit the establishment of rhythmical bodily motions soon experience a "mind freedom" which permits protracted reveries. Such reveries are often pleasurable mental excursions which leave the worker in an emotionally quiescent state. The triple combination of (a) response to measured cadence, (b) day dreaming, and (c) earning one's living, accounts for great masses of human beings remaining contented year after year at work which requires only muscular attention. Bodily response to rhythm, and mental tendency to day dream, are among the oldest habits of man. When a human being engages in age-old customs, a sense of satisfaction usually accompanies such acts.

Machine made reveries may consist of nothing more than idle and fanciful musings or even morbid worries. On the other hand, they may be meditations of great merit. Samuel Gompers and Michael Pupin are examples of men who planned great things while they were still uneducated routine workers and later in life made imperishable contributions in their respective fields. Each in his autobiography clearly traces such deeds to the "mind freedom" permitted by certain work in their early lives. A number of other cases of reveries on the job are cited, among them being the experiences of the investigator himself while a conveyor worker at the Ford Motor Company plant.

The paper concludes with the suggestion of further research into the possibility of directing the mind habits of rhythmical workers into more generally constructive channels.

The Check-list as an Instrument to Determine Personality Changes in Pre-school Children.—By W. G. PIERSEL, Marietta College.

The check-list used was devised by Dr. Elizabeth Moore of the Iowa Child Welfare Research Station, State University of Iowa. The activities, briefly stated, are these:

1. Shows alert curiosity.
2. Tries to mold environment to his purpose.
3. Finds interesting occupation.
4. Creates or constructs.
5. Plans definitely.
6. Exerts efforts at continued difficulty.
7. Gives sustained attention.
8. Faces issues frankly.
9. Rises to meet occasion.
10. Shows stability at changes in environment.
11. Speaks with cheerful, well-placed voice.
12. Shows self-control when mentally or physically hurt.
13. Shows composure at interference from others.
14. Sees humorous aspect of situation.
15. Shows ability to care for own needs.
16. Speaks and acts with directness and effectiveness.
17. Welcomes and uses help and advice.
18. Adjusts to social needs or order.
19. Shows kindness to others.
20. Shows healthy direction of affections.
21. Respects the rights of others.
22. Converses with others.
23. Shows sensitiveness to approbation.
24. Seeks companionship, responds to friendly advances.
25. Enters into cultural experiences.

Taking Phyllis as an example, six observations of fifty minutes each were made, and after checking, were divided into two equal parts, the first three coming early in the period, and the last three much later. A comparison of the scores in the two periods indicates certain positive changes in personality, such as increasing stability at changes in environment, more definite planning, giving sustained attention, and more seeing of the humorous aspect of things. A large increase in disobedience to adult requests is noted, which tends with the other changes to show increased capacity for self-direction. With added familiarity to the pre-school situation, she talks much more, expressing more ideas, and shows less tendency to seek the companionship of others.

Some Comments on the Interrelations of Intelligence Test Score, Stated Intention of going to College and Occupational Choice of High School Seniors.—By HAROLD A. EDGERTON, Ohio State University.

The data presented are from the study of over 30,000 Ohio High School seniors in the autumn of 1930. The following may be briefly noted:

1. There is some relation between an intelligence test score (Form 17, Ohio State University Psychological Examination) and stated intention of going to college.

2. There is too little differentiation between low scoring and high scoring pupils as regards intention of college attendance.

3. There is some relationship between the occupation which the pupil expects to enter and his test score. Such occupations as author, chemist, lawyer, physician, are chosen mainly by high scoring pupils; and occupations such as farmer, beauty parlor operator, machinist, carpenter are chosen by those of lower test score.

4. The data give some notion of the sort of intellectual competition the pupil will have to meet in entering the various occupations.

5. Most of the girls who have expressed an occupational preference, wish to enter one of three occupations: teaching—precollege (1851), nursing (1751), and stenography (2485).

6. The data, which have so far been studied, indicate that much time in high school should be spent in the guidance of:

(a) Girls generally.
(b) Boys and girls whose parents are not professional people.
(c) Girls who have decided to go into elementary or secondary teaching, stenography or nursing.
(d) Boys and girls who have not yet decided regarding college, particularly the brilliant and scholarly.
(e) Brilliant and scholarly boys and girls who have decided against college attendance on financial grounds.

PHYSICAL SCIENCES SECTION.

The Lecture-Demonstration and Individual Laboratory Methods of Introducing College Students to First Year Chemistry.—By C. C. Ross, University of Kentucky, and V. F. Payne, Transylvania College.

The study here reported involving twelve sections of first year college chemistry students in four institutions has not produced uniformly significant results. The writers have concluded, however, on the basis of several methods of comparison, the number of students used and the number of colleges and instructors involved, that these students made better progress, as that progress is commonly measured, when introduced to the study of college chemistry by the lecture-demonstration method. Likewise they have concluded that the students of lesser ability profited relatively more by the introduction through lecture-demonstration than did the students of greater ability. Also there were indications that later work by the individual laboratory method is strengthened by the lecture-demonstration introduction.